Phacopid trilobites in post-Taghanic Givetian through Frasnian cephalopod limestones, Montagne Noire (France) and related areas (Thuringia, Morocco)

Raimund Feist & Gilbert Klapper

This paper establishes the ranges of late Givetian and Frasnian phacopid trilobites with reference to the Frasnian conodont zonation. The ranges integrate both hitherto formally known and numerous new taxa that were recovered from outer shelf limestones primarily in the Montagne Noire (southern France) and incidentally in related areas; *i.e.* Thuringia and SE Morocco. Though considering twice the number of genera and species as previously known, the distribution of phacopids emphasises the generally admitted low diversity in the time interval between the Taghanic and Kellwasser crises. New evidence highlights the fact that diversity rates did not remain constant over the period but increased slightly in mid- and late Frasnian times. The currently proposed lower–middle Frasnian substage boundary at the base of the *punctata* Zone (FZ 5) is supported by two major innovations at the generic level. The investigated outer shelf phacopids are all characterised by reduced eyes with either a reduced visual surface or with forwardly positioned and diminutive eye lobes. In the systematic part the following taxa are presented: *Cronierella* gen. nov. with the new species: *C. gallica*, *C. postera*, *C. expansa*, *C.*? sp. nov. A; *Occitanella* gen. nov. with the new species: *O. postinflexa*, *O. hexagonalis*, and *O.*? sp. indeterminate; *Chlupacops* Feist, 2016 with the new species *C. angularis*, *C. narbonnensis*, *C. clapassousensis*, *C. migrans*, *C. rectannulatus*; *Acutiphacops* gen. nov. with the new species: *A. tchrafinensis*, *A. medius*; *Acuticryphops prorotundus* sp. nov.; *Girardina* gen. nov. with the new species: *G. konradbartzschi*, *G. consimilis*, and with *G.*? *liopyga* (Richter, 1863). • Key words: phacopid trilobites, late Givetian, Frasnian, conodont-based biostratigraphy, eye reduction, systematics.

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The late Middle Devonian Taghanic crisis (House 1985, Zambito *et al.* 2012) severely affected the evolutionary history of trilobites. After the demise of four families and six subfamilies shortly before and during the late middle Givetian event interval (Aboussalam 2003), trilobites experienced the lowest diversity rates in the Devonian (Feist 1991, Chlupáč 1994, Lerosey-Aubril & Feist 2012). In the Phacopidae this decline had already started at the end of the early Givetian when, from six genera with some 40 species present in the Rhenish Slate Mountains, Germany (Basse 1998, 2006), the only species that reached the middle Givetian were those questionably assigned to *Hypsipariops* such as *H.*? *torleyi* (Basse & Lemke, 1996) and *H.*? *batracheus* (Whidborne, 1889) from the famous Lummaton shell-bed in southern England, as well as descendants of *Chotecops*, the *koeneni* group (Meischner 1965, Basse & Lemke 1996). These taxa vanished at the Taghanic crisis. In eastern and midcontinent North America "*Phacops*" *iowensis* and subspecies of the widespread Middle Devonian *Eldredgeops rana* were still present prior to the Taghanic Event, but only the latter survived the crisis (Eldredge 1972). Based on the paucity of phacopids in the interval between the end mid-Givetian Taghanic and the terminal Frasnian Kellwasser events, the generally low diversity trend was thought to affect likewise the Phacopidae with only a few innovations (Lerosey-Aubril & Feist 2012). That view is revised here after discoveries of numerous new taxa mainly from the Montagne Noire that double the number of those hitherto known. Taking into account all formally recognized taxa these are listed according to their biostratigraphical occurrences (Fig. 1). Most of them are well constrained by associated conodont zonal markers and can be assigned to conodont zones (Fig. 1, bold lines). However, their occurrences might not range through the entire zone, or alternatively, their ranges might extend beyond a single

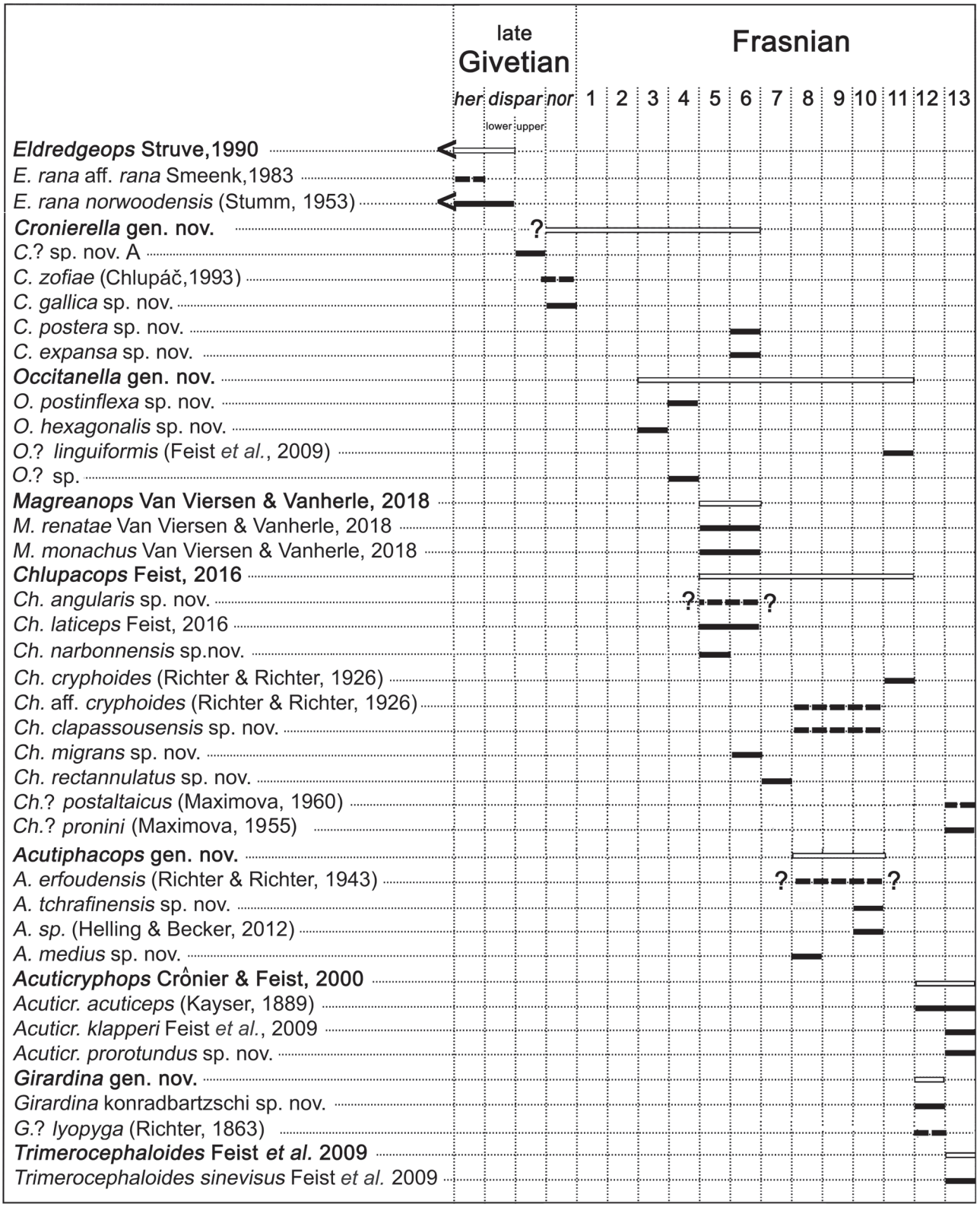


Figure 1. Range chart of late Givetian through Frasnian Phacopidae according to conodont biozonation (*her* – *hermanni* Zone; *dispar* – *disparilis* Zone; *nor* – *norrisi* Zone). Explanation: bold lines – known occurrences; empty lines – inferred occurrences; dashed lines – presumed ranges; question marks – possible extensions; arrows – extensions below upper Givetian.

zone. In contrast, zonal assignment of other taxa remains undetermined when no significant conodonts were associated (Fig. 1, dashed lines); their biostratigraphical ranges according to the conodont zonation are tentative and need further investigation. Whereas seven out of nine genera from the considered time interval occur in at least two different palaeogeographic entities (Crônier & François 2014), 55% of the species are restricted to the Montagne Noire, virtually indicating a high degree of endemism but calling for further search in similar outer shelf sites of neighbouring regions.

Biostratigraphy and location

Late Givetian occurrences

Hitherto known post-event occurrences of phacopids in Variscan Europe in the late Givetian remained extremely scarce, restricted to two taxa of *Eldredgeops rana* affinity recognized in the southern Cantabrian Mountains (Smeenk 1983). In midcontinent North America only *Eldredgeops rana norwoodensis* persisted in the late Givetian (Hickerson 1997). In Australia a single phacopid cephalon from the late Givetian or possibly early Frasnian Mytton Formation in the Broken River region of North Queensland was described by Feist & Talent (2000) as *Phacops* sp., but the poor preservation does not allow confident assignment. Stegemann (2005) described and figured the first late Givetian phacopid remains from Morocco that she assigned to unnamed new subspecies of *Hypsipariops*? *torleyi*. Though listed in the compendium of North African trilobites by Bault *et al.* (2021), the material needs revision taking into account the configuration of the intercalating ring that obviously differs from that of *Hypsipariops* and *torleyi*. In the Holy Cross Mountains, Chlupáč (1993) described *Phacops* (*Chotecops*) *zofiae* from the Givetian–Frasnian boundary beds at Szydłówek, which we assign to the new genus *Cronierella* from the topmost Givetian and lower Frasnian. To date, only two genera (*Eldredgeops* and *Cronierella*) are recognized with confidence in the late Givetian. Among them, the appearance of *Cronierella* seems to constitute a slight recovery from the Taghanic crisis no earlier than at the end of the Givetian (Fig. 2). Though further new occurrences in Moroccan strata are expected (see Aboussalam & Becker 2001 for presence of phacopids in the *hermanni* Zone at Bou Tchrafine), the rather poor record confirms the extremely low diversity with the probable extinction of *Eldredgeops* and a single innovation at the end of the Middle Devonian.

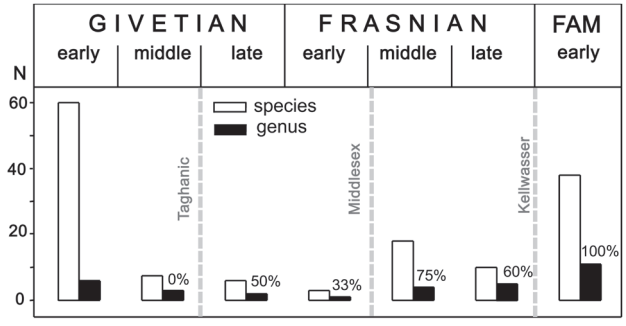


Figure 2. Diversity trends of phacopid species between early Givetian and early Famennian indicating the position of the Taghanic, Middlesex and Upper Kellwasser events (empty columns – number of species; bold columns – number of genera). Generic innovation rates are given in percentage of total number.

Frasnian occurrences

The paucity of phacopids that characterises the late Givetian was considered to persist into the early Frasnian where only a single phacopid was recovered from "Chemung" sandstones of New York (Eldredge 1972, p. 93), probably from the Ithaca Sandstone of FZ 2–3 age (Klapper & Kirchgasser 2016). This taxon, referred to *Eldredgeops rana rana* by Eldredge, led to the assumption that *Eldredgeops* persisted into the Late Devonian (Crônier & François 2014). However, besides the fact that this material was not located stratigraphically with precision, it was neither figured nor described. Thus its assignment remains doubtful and it is not considered here. *Cronierella*, though appearing just below the G–F boundary, has not yet been identified in early Frasnian strata but reappears in the middle Frasnian (FZ 6). The new genus *Occitanella* with two (three?) species from the Montagne Noire is the only taxon currently known in the early Frasnian. The substage has the same low innovation rate as that of the late Givetian. As such it confirms the lowest diversity for trilobites in general (*e.g.* for North African occurrences, Bault *et al.* 2021). In phacopids the curve of low diversity trends greatly changes when two genera, *Chlupacops* and *Magreanops*, appear at the base of the middle Frasnian (Feist *et al.* 2016, Van Viersen & Vanherle 2018). Together with the reappearance of *Cronierella* and the appearance of the new genus *Acutiphacops* in the higher part of the substage, there are four genera with 18 species present in the middle Frasnian. However, among this relatively high number of taxa at the specific level, some cannot be precisely attributed to conodont zones (marked by dashed lines in Fig. 1) mainly because of the absence of significant conodont data. In some cases the presumed stratigraphical position remains doubtful (taxa marked with question in Fig. 1) and needs confirmation from new investigations. This concerns in particular the position of *Acuticryphops erfoudensis* that Richter & Richter (1943) described from material collected by the Termiers

in the 1930s in the surroundings of Erfoud (Tafilalt, SE Morocco). On the basis of its morphological proximity to *Acutiphacops* taxa from the late middle Frasnian of Bou Tchrafine a similar age attribution is tentatively presumed. Increase of diversity is corroborated in the late Frasnian where, in addition to the entry of two previously known genera, the new genus *Girardina* appears simultaneously in the Montagne Noire and in eastern Thuringia. Both *Occitanella* (?) and *Chlupacops* persist in the late Frasnian with a single species each. To the latter might be assigned with question two species from the Rudny Altai and from the eastern slope of the middle Urals: *Ch*.? *postaltaicus* Maximova, 1960 and *Ch*.? *pronini* Maximova, 1955 respectively. The biostratigraphical position of the latter species, occurring in the "*Crickites* Zone" according to Maximova (1955, p. 193), raises the question of whether an earliest Famennian ("post Iδ") age could be considered (Feist 2019). However, the species is said to be associated with the last scutelluids that became extinct at the terminal Frasnian Kellwasser crisis. Consequently, both *Ch.*? *pronini* as well as *Ch.*? aff. *pronini* (the latter being associated with *postaltaicus*) are probably of latest Frasnian age though no conodont control is available. To sum up, five genera with 10 species are present in the late Frasnian. The reversal from initially very low diversity rates to positive trends initiated in the mid-Frasnian is corroborated at the end of the stage (Fig. 2). The terminal Frasnian Kellwasser Event severely affected the Phacopidae as no lower rank taxon survived into the Famennian (McNamara & Feist 2016). In sharp contrast the early Famennian recovery is characterised by high innovation rates when five new genera with some 38 species successively appear (Feist 2019).

The biostratigraphical significance of the Phacopidae in the Frasnian in terms of discriminating currently debated positions of substage boundaries may be partially important. Whereas the initial pulse of the Frasnes Event in the terminal Givetian *norrisi* Zone (Becker *et al.* 2020) coincides with the innovation of the *Cronierella* line, the exact position of the Givetian–Frasnian boundary cannot be discriminated as any innovation is currently unknown at the beginning of the Frasnian. By contrast, the base of FZ 5 (Middlesex transgression or *punctata* Event) is well marked by the concomitant innovation of *Magreanops* in the organodetrital inner-shelf realm and *Chlupacops* in the off-shore cephalopod realm. Allowing time-scaled correlation between the two realms the appearance of these phacopid biostratigraphical markers supports defining the middle Frasnian substage at the base of the *punctata* Zone (Fig. 2). By contrast, the start of the proposed late Frasnian substage with the *semichatovae* Event just slightly above the base of FZ 11 (see Conodont Zonation) is less well supported as only two species appear at this level. Major innovations in the Phacopidae occur a little higher, when *Acuticryphops* and *Girardina* appear in FZ 12 and *Trimerocephaloides* in FZ 13.

Frasnian conodont zones and events (G. Klapper)

The thirteen-fold Frasnian conodont zonation (abbreviated as FZ) was established originally through the analysis of overlapping species ranges in six measured sections (Feist & Klapper 1985, Klapper 1985) in the Montagne Noire (Klapper 1989). The ranges of all short-ranging conodont species, including those of *Ancyrodella*, *Ancyrognathus* and *Ozarkodina*, were used in developing the zonation in addition to those of *Palmatolepis*, the first occurrences of which define the majority of the bases of zones. As has been demonstrated in subsequent studies, the zonation is not confined to the Montagne Noire but has been tested and demonstrated to be widely applicable in Devonian tropical areas. These include among others, the Canning Basin of Western Australia (Klapper 2007, 2009), the Alberta Rockies and central Alberta subsurface, western Canada (McLean & Klapper 1998), and the classic sections of western New York State (Kirchgasser 1994, Kralick 1994, Klapper & Kirchgasser 2016). Because of its widespread application, Klapper & Kirchgasser (2016) recommended a significant change in terminology from the Montagne Noire (MN) zonation to the Frasnian Zonation (FZ).

The Frasnian Zonation was integrated with graphic correlation through studies of sequences, for example the Timan Range of European Russia (Klapper *et al.* 1996), Luscar Mountain in the Alberta Rockies, the Hay and Trout river areas of southwestern Northwest Territories (Klapper 1997), the Moose River Basin, northern Ontario (Klapper *et al.* 2004), all in Canada, and western New York (Klapper *et al.* 1995, Klapper & Kirchgasser 2016).

In the restudy of the Martenberg section in the Rhenish Slate Mountains, one of the key sections of the Frasnian Standard Zonation of Ziegler & Sandberg (1990), the *transitans* through *linguiformis* zones were shown to correlate with FZ zones 4 through 13 (Klapper & Becker 1999, text-fig. 1). The FZ 13 spans from the upper *rhenana* through *linguiformis* zones of the standard zonation, and thus because of its long span was subdivided into three subzones (Girard *et al.* 2005).

The Middle Devonian (late Givetian) zones shown in Figure 1 correspond to the usage of Klapper & Johnson (*in* Johnson 1990), in ascending order: *hermanni*, lower and upper *disparilis*, and *norrisi* zones. Bold lines in this figure indicate joint occurrences of the zonal conodonts with the trilobites.

In regard to intra-Frasnian events, much discussed in recent Devonian literature, the base of FZ 5 (= *punctata*

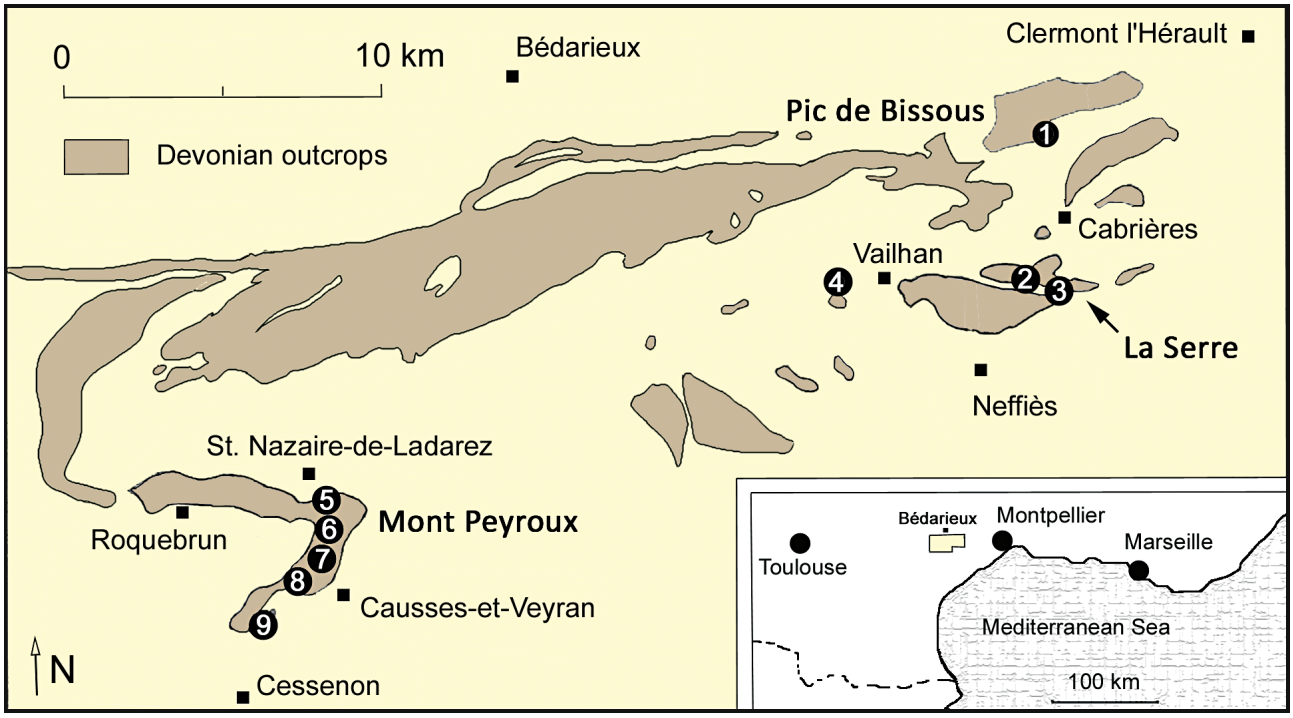


Figure 3. Location of conodont-dated phacopid sites in Devonian outcrops of southeastern Montagne Noire (1 – Pic de Bissous; 2 – Soureillé d'Izarne; 3 – La Serre; 4 – Combe Rolland; 5 – Col du Puech de la Suque; 6 – Clapassous; 7 – Mont Peyroux; 8 – Causses-et-Veyran; 9 – Coumiac). For locality register see text.

Zone of Ziegler & Sandberg 1990) was thought to coincide with the Middlesex Event, one of the two main transgressions within the classic New York State Frasnian succession. The correlation of the base of the *punctata* Zone with the Middlesex Event in the Rhenish Slate Mountains and Polish sections (*e.g.* Pisarzowska *et al.* 2020) was based on using the FAD of *Ancyrodella nodosa* (= *A. gigas* form 1 of earlier literature) for that identification, rather than *Palmatolepis punctata* (shown in Pisarzowska *et al.* 2006, tabs 5, 6) and as discussed in their 2020 paper (*op. cit.*, p. 4). *Ancyrodella nodosa* as revised in Klapper & Kirchgasser (2016, p. 537, tab. 2) occurs only a short interval below the base of FZ 5 in terms of graphic correlation; this means that its FAD is within the upper part of FZ 4 (= *transitans* Zone). Its illustrated occurrence in the upper 2 cm of the Middlesex at Eighteenmile Creek (Over *et al.* 2003, pp. 218, 219, pl. 1, fig. 5) is close below the entry of *Palmatolepis punctata* in the overlying basal Cashaqua Shale. The details of its lower range within the Middlesex (*op. cit.*, fig. 2) are not given.

The major transgression within the New York Frasnian sequence begins at the base of the Rhinestreet Shale and was earlier taken as the second intra-Frasnian event (House 2002, p. 17 and references therein). However, Sandberg *et al.* (2002, p. 479) used the *semichatovae* transgression, which is based on the FAD of this species of *Palmatolepis*, as a signficant intra-Frasnian event. It seems now to be widely used. In the New York succession, the *semichatovae* FAD occurs in the higher part of the Rhinestreet at the Relyea Creek Horizon (Klapper & Kirchgasser 2016, figs 5, 6, tabs 1, 2) and is slightly less than one composite standard unit in graphic correlation above the base of FZ 11.

Location of occurrences

Montagne Noire occurrences. – In the south-eastern Montagne Noire nine localities have yielded late Givetian and Frasnian phacopid trilobites (Fig. 3). Associated conodonts and conodont ranges in columnar sections were determined by G. Klapper. Locality register follows Klapper (1989, pp. 456, 457) and is supplemented herein. Coordinates are calculated from Google Earth mapping.

(1) Pic de Bissous, section VS-E, deep slope at 150 m southwest of the peak, at 2.3 km north of Cabrières, 43° 35′ 49.19″ N, 3° 21′ 16.68″ E. Location and columnar diagram of the sequence is shown in Feist (1983, fig. 13), Feist & Klapper (1985, figs 3, 5) and Klapper (1985, fig. 1). Phacopid occurrences in bed 49: *Occitanella hexagonalis* gen. and sp. nov., Frasnian Zone 3.

(2) Soureillé d'Izarne section, southern flank of hill, at 2 km SW of Cabrières, 300 m N of La Rouquette farm house, stop 10 in Feist (1983). Phacopid locality: 43° 33′ 29.09″ N, 3° 21′ 02.32″ E, = *Acuticryphops prorotundus* sp. nov.

(3) La Serre trenches A, A' and C, on the southern flank of the east-west oriented La Serre hill, south and south-east of the western summit 252, at 2.2 km south of Cabrières. A, A' = 43° 33′ 24.43″ N, 3° 21′ 20.06″ E, 500 m east-northeast of La Rouquette farm house. Location and columnar diagrams are shown in Feist (1983, figs 19, 20), Feist & Klapper (1985, figs 4, 5, 8, 9) and in Feist (2002, fig. 30b). Phacopid occurrences: bed A 102C, A'17 ("lumachelle à phacopidés" of Feist 1976, "*Phacops*-bed" of Feist 1983, 1985) = *Cronierella gallica* gen. and sp. nov., Givetian *norrisi* Zone; bed A 129 and A'42 = *Cronierella expansa* gen. and sp. nov., Frasnian Zone 6; bed A 133 = *Cronierella postera* gen. and sp. nov., Frasnian Zone 6; bed A'48 = *Chlupacops migrans* sp. nov., Frasnian Zone 6; A'60 = *Chlupacops rectannulatus* sp. nov., Frasnian Zone 7; A'71 = *Acutiphacops medius* gen. and sp. nov., Frasnian Zone 8. C = 43° 33′ 21.77″ N, 3° 21′ 35.56″ E, 650 m east-northeast of La Rouquette farm house. Location and columnar diagrams are shown in House *et al.* (1985, fig. 12), Feist (1990, fig. 28; 2002, fig. 31). Phacopid occurrences: bed 13 = *Acuticryphops prorotundus* sp. nov.

(4) Combe Rolland, road-section at 1.5 km W of Vailhan. Phacopid locality: 43° 33′ 03.11″ N, 3° 17′ 07.83″ E = *Acuticryphops prorotundus* sp. nov.

(5) Col du Puech de la Suque, CPS-E section, natural outcrops about 50 m east of the crest of hill 358 at 700 m SE of St Nazaire-de-Ladarez, 43° 30′ 11.46″ N, 3° 05′ 11.19″ E. Location and columnar sections are shown in Feist (1983, figs 9, 10), Klapper (1985, fig. 2), Feist & Klapper (1985, figs 2, 5), House *et al.* (1985, figs 1b, 2) Klapper *et al.* (1987, fig. 1) and Feist (2002, fig. 21). Phacopid occurrences in CPS-E: *Occitanella postinflexa* gen. and sp. nov., *Chlupacops angularis* sp. nov., *Chlupacops narbonnensis* sp. nov.

(6) Clapassous, western slope of Puech de la Suque hill, 300 m SSE of CPS-E section, at 1 km SE of St Nazaire-de-Ladarez, 43° 30′ 03.53″ N, 3° 05′ 19.91″ E = *Chlupacops clapassousensis* sp. nov., *Ch. migrans* sp. nov.

(7) Mont Peyroux, Col des Tribes Sud section (CT-S), eastern slope at 200 m E of summit, at 2 km SE of St Nazaire-de-Ladarez, 43° 29′ 24.72″ N, 3° 06′ 22.07″ E. Location and columnar sections are shown in Dartiguenave (1999, figs 2, 6, 9) and Aboussalam (2003, fig. 30). Phacopid occurrences: *Cronierella*? sp. nov. A, *Occitanella*? sp.

(8) Causses-et-Veyran, 500 m NW of village, at about 100 m NE of section CV-S (Feist 1990, figs 10–12), 43° 28′ 45.38″ N, 3° 04′ 48.64″ E = *Acuticryphops acuticeps* (Kayser, 1889), *Girardina consimilis* gen. and sp. nov.

(9) Coumiac, abandoned marble quarry at 2 km N of Cessenon, upper quarry at 200 m west of 'Les Granges" farm house, 43° 28′ 13.86″ N, 3° 03′ 35.38″ E. Location and columnar sections are shown in Feist (1983, figs 7, 11), Feist & Klapper (1985, figs 2, 5), House *et al.* (1985, figs 1a, 9), Becker *et al.* (1989, figs 1–3), Feist (1990, figs 17–21). Phacopid occurrence: *Acuticryphops acuticeps* (Kayser, 1889).

Moroccan occurrence. – Bou Tchrafine at 9 km SE of Erfoud, Tafilalt, SE Morocco, 31° 22′ 34.53″ N, 4° 09′ 59.44″ E. Location and columnar sections are shown in Buggisch & Clausen (1972, fig. 2), Bultynck & Walliser (2000, figs 1, 8), Becker & House (2000, fig. 1). Phacopid occurrences: *Acutiphacops tchrafinensis* gen. and sp. nov., *Acutiphacops erfoudensis* (Richter & Richter, 1943)

Thuringian occurrence. – Abandoned Kahlleite quarry at 6 km NE of Schleiz, 50° 37′ 40.90″ N, 11° 50′ 51.46″ E. Location and columnar section shown in Gereke (2007, figs 29, 35). Phacopid occurrences: *Acuticryphops acuticeps* (Kayser, 1889), *Girardina konradbartzschi* gen. and sp. nov. Bohlen section at 1.5 km S of Saalfeld, 50° 37′ 60″ N, 11° 22′ 52″ E. Location and columnar section shown in Pfeiffer (1954, tab. 1). Phacopid occurrences: *Chlupacops cryphoides* (Richter & Richter, 1926); Laasen (Probstzella), Köppchen, 259 m NW Laasen (*fide* Pfeiffer 1959): *Girardina*? *liopyga* (Richter, 1863).

Palaeontology (R. Feist)

Trends in eye reduction

One of the common morphological features of Silurian through Middle Devonian Phacopidae is the development of large kidney-shaped eyes with a great number of lenses arranged in vertical rows. Phacopids of this kind occur in various types of organodetrital facies of shallow neritic environments but also in deeper, mostly micritic limestone facies where they lived on the muddy sea floor within the photic zone (Chlupáč 1977). Such phacopids were markedly restricted in their diversity in the late Givetian where only representatives of *Eldredgeops*

survived the Taghanic crisis and occur in midcontinent North America and in the Cantabrian Mountains. The so-far unique presence of large-eyed phacopids in the Frasnian was recently brought to light by Van Viersen & Vanherle (2018) in early mid-Frasnian lateral facies of sea mounds in the Ardennes. This important discovery bears witness that the ancestral configuration of a large-sized eye complex must have persisted in shallow neritic environments allowing their epibenthic activity in photic bottom habitats. The advent of *Cronierella* in the terminal Givetian marks the first hint of eye-reduction in the large-eyed configuration, when the dorsoventral height of the visual field diminishes and the number of lenses in vertical rows reduces to four lenses. The posterior end of the eye lobe is markedly reduced in height whereas its exsagital length remains unchanged.

Eye reduction leading to forward shift and diminishing in size of the eye lobe became a general phenomenon in Frasnian Phacopidae. When similar cases of eye reduction occur in some older taxa from the Lower and Middle Devonian (e.g. *Eocryphops*, *Struveaspis*, *Prokops*) they were considered to be environmentally controlled, as these forms preferentially inhabited poorly consolidated, quiet, muddy substrates in deeper water (Chlupáč 1977 and other authors). Their occurrences are sporadic and recurrent in various time intervals and their mode of regression of the visual surface ("*cryptophthalmus* pattern", Richter & Richter 1926) seems not to follow any generalised evolutionary trend. Small advanced eyes that characterise most Frasnian phacopids in outer-shelf limestones are already developed in Early Devonian *Reedops*, which however have a much higher visual surface with significantly more lenses that are perfectly arranged in vertical rows. Similarly, the early Middle Devonian *Chotecops* exhibits advanced eye lobes leaving a conspicuous postocular space on the genal field. Whereas these forms occur in both biodetrital and muddy micritic biotopes, the descendant *Chotecops koeneni* group in the middle Givetian was exclusively adapted to off-shore cephalopod- and stylioline-bearing calcilutites. Following the Taghanic onlap this biotope became dominant in outer shelf domains of southern Europe and North Africa as well as on submarine rises in the Rhenish Slate Mountains and Thuringia. In these domains evolutionary trends towards eye reduction occur most commonly not only in the Phacopidae but also in the Proetida (*e.g*. Feist 1995). Most Frasnian phacopid genera are characterised by advanced eye lobes with low kidney-shaped visual surfaces with irregularly packed lenses arranged in vaguely discernible vertical rows. Initiated by *Occitanella* in the late early Frasnian this configuration remains relatively stable in numerous mid-Frasnian species of *Chlupacops* and *Acutiphacops* with only minor variation in the size of the ocular complex and the post-ocular distance from the posterior border of the cephalon. Successive populations of *Acuticryphops acuticeps* show a continuous reduction in mean lens numbers (Feist 1995, Crônier *et al.* 2004), whilst the original reniform visual surface, still developed in early morphs, assumes an elliptical outline of lens arrangement when the number of lenses decreases below eleven. At this stage of the *cryptophthalmus* pattern the remnant palpebral lobe has become minute and subtriangular, whereas its distal edge tends to straighten in upper view and to curve upwards in anterolateral view. Morphs in which a single lens remains are frequent in topmost Frasnian levels but the presence of blind morphs has not been established prior to the extinction event at the Upper Kellwasser horizon. As yet the only blind taxon from the Frasnian is *Trimerocephaloides* from FZ 13a of the Canning Basin (NW Australia) (Feist *et al.* 2009). Though devoid of any lenses, remnants of (functional?) ocular devices are still perceptible in the form of minute protuberances crossed by the facial suture in the anteriormost adaxial corner of the cheek. Such configuration is reminiscent of some species of early Famennian *Pulvinocephalus*, *Trifoliops* and *Trimerocephalus* though direct phyletic links between these taxa to latest Frasnian ones have not been established with certainty (Feist 2019).

Aspects of phyletic relations and morphological traits

The origin of the Late Devonian Phacopidae remains obscure due to the poor knowledge of representatives in the late Givetian. Regardless of the low eye lobes in *Cronierella* that might result from paedomorphic processes, many features of the cephalon such as the outline and vault of the glabella and the configuration of the intercalating ring are very close to late representatives of *Eldredgeops*. However possible phyletic links between these genera are contradicted by the fact that the pygidia are quite dissimilar and the question of phyletic relationships remains open until new discoveries of related taxa are made in late Givetian strata. Search for similarities based on traits of the cephalon alone are often biased by homeomorphy whereas morphological features of the pygidium in Late Devonian phacopids are obviously more stable and characteristic for defining genera. Changes in their morphology in the Frasnian concern essentially the axis that shortened to remain considerably distant from the posterior edge. This is perceptible in younger species of *Cronierella* in comparison to the initial species from the latest Givetian. It is more conspicuous in *Occitanella* and *Girardina*. The prolongation of the posterior end of the axis by a marked post-axial ridge as in *Cronierella* and *Occitanella* is outstanding in the Phacopidae, and as such

may constitute an innovation. By contrast the pygidia of *Chlupacops* are devoid of postaxial ridges, but the axial furrows remain unclosed beside the rounded posterior tip of the axis. These are closed though shallow around the end of axes in both *Acutiphacops* and *Acuticryphops*, and remain unchanged in depth in *Girardina*.

Some early Famennian taxa such as *Nephranops* were considered by Chlupáč (1977) to be related to *Chotecops*, that was thought to persist into the Late Devonian with its putatively last representatives "*Phacops*" *nalivkini* Maximova, 1955 and "*Phacops*" *pronini* Maximova, 1955, both taxa being later tentatively reassigned respectively to *Houseops* Feist *et al*., 2009 and to *Chlupacops* (herein). The presumably last representatives of *Chotecops* constitute the mid-Givetian *koeneni* group, comprising *Ch. koeneni* (Holzapfel, 1895), *Phacops* s.l. (*Ch*.?) sp. n. aff. *koeneni* Basse & Lemke, 1996 and *Ch. spectabilis* (Meischner, 1965), the latter probably being a synonym of *koeneni*. However, these taxa exhibit markedly smaller and more advanced eyes than the typical Eifelian species and allies. By these features the *koeneni* group is closest to representatives of *Chlupacops* and as such was questionably included in the latter by Feist *et al.* (2016). However there is a considerable time interval of some 3 Ma between the late mid-Givetian Taghanic extinction of the *koeneni* group and the first *Chlupacops* in the mid-Frasnian (FZ 5), devoid of any morphologically intermediate taxa that would testify to possible direct evolutionary links between *Chotecops* and *Chlupacops*. Before more and better preserved material of the former would allow exhaustive evaluation of specific characters to be made, Chlupáč (1977) is followed in assigning the *koeneni* group to *Chotecops*, and considering this group the root stock of the Frasnian representatives of *Chlupacops*. As such and according to the scheme of phylogenetic development proposed by Chlupáč (1977, fig. 26) the *Chotecops* – *Chlupacops* line gave rise to the early Famennian *Nephranops*, and in particular to *N.* (*Maternia*) Feist, 2019, by extreme reduction until obsolescence of eye lenses on the visual surface. In addition, it gave rise also to other Famennian phacopids such as *Houseops* that shares with *Chlupacops* the anteriorly wide glabellar lobe, the advanced eye and the short pygidial axis.

Members of the phyletic lineage leading from *Acuticryphops* to *Trimerocephalus* suggested by many authors (*i.e.* Chlupáč 1977 and Feist 1995) are characterised by backwardly directed pre-vincular doublure, frontal overhang of the anteriorly pointed glabella in the cephalon, and a transverse pygidium with low and short axis. This configuration is partially developed in *Acutiphacops* which is considered the direct ancestor of *Acuticryphops*. However, the former is distinct through features that are typical for *Phacops* s.l., such as the narrow cylindrical border and deep border furrow, as well as the long postvincular doublure. Whether the suggested direct ancestor-descendant relation existed between *Phacops* and the *Acuticryphops–Trimerocephalus* line (Chlupáč 1977, fig. 26), with *Acutiphacops* as an intermediate, cannot be excluded but further knowledge of potentially intermediate taxa from the Givetian and early Frasnian is needed. Likewise, the question of ancestry of *Occitanella* and *Girardina* remains problematic and currently unsolved.

Systematic paleontology

Terminology follows Whittington & Kelly (1997) and McKellar & Chatterton (2009). Measurements of pygidial length do not include the articulating half ring.

Depository: UM-IP – University of Montpellier; Invertebrate Palaeontology (UM-IP 858–961).

Order Phacopida Salter, 1864
Family Phacopidae Hawle & Corda, 1847
Subfamily Phacopinae Hawle & Corda, 1847

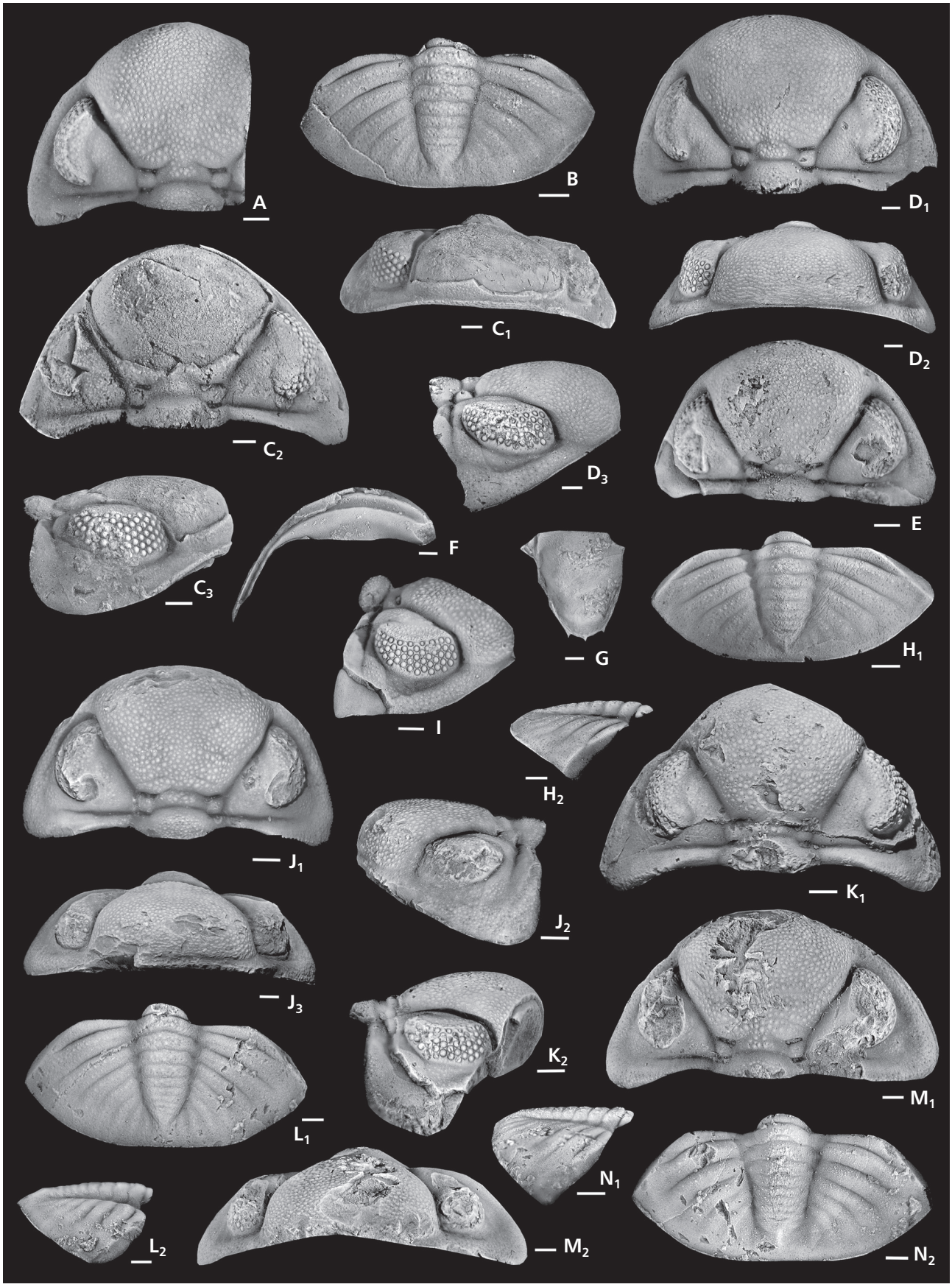
Genus *Cronierella* gen. nov.

Type species. – *Cronierella gallica* sp. nov.

Etymology. – After Catherine Crônier (Lille) in recognition of her substantial work on Late Devonian phacopids.

Diagnosis. – Glabella moderately vaulted, not overhanging in front; palpebral furrow shallow; low eyes remaining in short distance from posterior border furrow, visual

Figure 4. All specimens from Montagne Noire, France. • A, B, D–I – *Cronierella gallica* sp. nov., La Serre.; A – fragmentary cephalon UM-IP 858, dorsal view; B – pygidium UM-IP 860, dorsal view; D – holotype cephalon UM-IP 862, anterior (D_1), dorsal (D_2), lateral (D_3) views; E – cephalon UM-IP 863, dorsal view; F – cephalon UM-IP 864, exfoliated, ventral view; G – hypostome UM-IP 866, ventral view; H – pygidium UM-IP 867, dorsal (H_1), lateral (H_2) views; I – fragmentary cephalon UM-IP 865, oblique lateral view. • C – *Cronierella*? sp. nov. A, eastern slope of Mont Peyroux; cephalon UM-IP 861, dorsal (C_1), anterior (C_2), lateral (C_3) views. • J–L – *Cronierella postera* sp. nov., La Serre; J – holotype cephalon UM-IP 872, dorsal (J_1), lateral (J_2), anterior (J_3) views; K – cephalon UM-IP 874, anteriorly fragmented, dorsal (K_1), lateral (K_2) views; L – pygidium UM-IP 875, dorsal (L_1), lateral (L_2) views. • M, N – *Cronierella expansa* sp. nov., La Serre; M – holotype cephalon UM-IP 876, dorsal (M_1), anterior (M_2) views; N – pygidium UM-IP 877, lateral (N_1), dorsal (N_2) views. Scale = 1mm.


A
B
D1
C1
D2
C2
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E
C3
F
G
H1
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K1
J2
J3
K2
M1
L1
N1
L2
M2
N2

surface considerably reduced in height at the posterior end, with 16 rows of lenses containing a maximum of four (five?) lenses; pygidium transverse subpentagonal; axis narrow, low, with eight rings, with distinct postaxial ridge not reaching posterior edge; pleural field moderately vaulted with six to seven flat ribs defined by deep pleural furrows not reaching lateral margin. Sculpture of flat tubercles becoming elongated on frontal face of glabella, exoskeleton pitted.

Remarks. – The new genus regroups phacopine taxa with moderately inflated cephala with long, low eyes, and transverse pygidia with narrow, low axis not reaching the posterior edge. The outline and vault of the glabella and palpebral area bear resemblances with *Eldredgeops* and, in particular, with *E. rana milleri* from the Givetian Silica Formation, Michigan. Characters in common are the modest transverse vault of the glabella without anterior overhang, and the distinctly tri-lobed intercalating ring. *Cronierella* gen. nov. shares with the *rana* group in particular: absence of subocular ridge and subocular pad, wide palpebral area and lobe, shallow palpebral furrow, moderately inflated glabella with vertical front wall, and rectangular lateral nodes on the intercalating ring. Consistent differences concern the much lower eye lobe remaining below the level of the glabella and the outline of the visual field which is "pointed" behind. Whereas the number of vertical rows of lenses (16) in *Cronierella* occurs in members of *Eldredgeops* (15–18) and notably in *E. rana milleri*, the number of lenses per row is much higher in the latter. A specimen from the Tully Formation assigned to *E. rana norwoodensis* (Eldredge 1972, fig. 15d) has a similar number of lenses including one row with 5 lenses. I agree with A. Van Viersen (written communication) that this specimen is different from the type species of *E. rana norwoodensis* which is characterised by a significantly higher number of lenses in a row (4–6) (Eldredge 1972, fig. 15b). The pygidia of the new genus differ from *Eldredgeops* in their general shape, and the low, narrow axis with postaxial ridge that does not reach the posterior edge.

Occurrence. – Montagne Noire, France, Holy Cross Mts. Poland; latest Givetian (Upper *disparilis*?) *norrisi* Zone through lower Frasnian Zone 6.

Species included. – *Cronierella gallica* sp. nov., latest Givetian *norrisi* Zone; *C. postera* sp. nov., Frasnian Zone 6; *C. expansa* sp. nov., Frasnian Zone 6; all from La Serre, Montagne Noire. *Cronierella zofiae* (Chlupáč, 1993), latest Givetian, basal Szydlówek Formation, Holy Cross Mountains, Poland. Questionably assigned: *Cronierella*? sp. nov. A, Col des Tribes, Montagne Noire, late Givetian, Upper *disparilis* Zone.

***Cronierella gallica* sp. nov.**
Figure 4D–I

Holotype. – Cephalon UM-IP 862, La Serre, Montagne Noire, *norrisi* Zone (Fig. 4D).

Type horizon and locality. – Microsparitic grey-brown trilobite coquina ("*Phacops*-bed"), Serre Formation, lower member (Feist 1985); La Serre hill, trench A'17, *norrisi* Zone, latest Givetian (Feist 1983, Feist & Klapper 1985).

Other material. – Paratypes: cephala UM-IP 858, 863–865; hypostome UM-IP 866; pygidia UM-IP 860, 867; additional material: nine cephala (UM-IP 868), a hypostome (UM-IP 869), a thoracic segment (UM-IP 870), seven pygidia (UM-IP 871), all from type horizon and locality.

Etymology. – *Gallicus* [Lat.] = from Gaul.

Diagnosis. – Glabella with high frontal wall; median lobe of distinctly tripartite intercalating ring ellipsoid, prominent; S1 curved forwards adaxially and interrupted medially; pygidium short, posterior outline wide parabolic, projection of maximum width opposite fourth axial ring. Axis long, slender, narrow anteriorly, pointed posteriorly; pleural field with seven low-vaulted ribs.

Description. – Cephalon distinctly longer than half width (58% of width), moderately vaulted transversely, gently curved anteriorly. Degree of glabella divergence is moderate (60°–65°). Anterior glabellar width more than twice width of intercalating ring, moderately vaulted, stronger in front where the height of glabella reaches 58% of length of its anterior lobe. Front wall of anterior glabella is high, slightly inflated, and does not overhang anterior border. Anterior border is framed by a thin, incomplete rim. Glabellar furrows S2 and S3 very thin, conspicuous but unimpressed in exoskeleton. Intercalating ring is markedly tripartite. Median lobe ovoid, inflated, carrying numerous tubercles, merging anteromedially with base of anterior glabellar lobe, distally separated from lateral lobes by broad, smooth depressions. Lateral lobes of intercalating ring largely subquadrangular with distinct adaxial edge, swollen, ornamented with small tubercles. S1 furrow directed forward adaxially, medially effaced. Occipital furrow gently rounded. Occipital ring twice as long as median lobe of intercalating ring, narrow (30% of cephalic width), without lateral lobes. Vincular furrow gently curved, deep, distinct, abaxially narrowing to become a deep narrow grove with almost inconspicuous notches. Postvincular doublure is depressed posteriorly, with slightly downturned edge at hypostomal suture. Palpebral area wide, poorly inflated. Palpebral furrow faint, weak in smaller specimens. Palpebral lobe is wide, slightly swollen, about

level with adaxial region of palpebral area. Eye is low, remaining below surface of anterior glabella, reaches anterolateral border furrow. Postocular genal field is half length (exsag.) of adjacent posterior border. Visual surface has 16 vertical rows of lenses with a maximum number of four lenses. Sclera in eyes thin throughout without sculpture. Base of visual surface lacks tubercles. Subocular groove has no pad. Subocular area of gena is narrow, slightly swollen, more so anterior to suture than posteriorly. Posterior branch of facial suture distinct. Posterior border furrow deep adaxially, fading away distally, very weak when meeting lateral border furrow in obtuse angle. Lateral border slightly inflated in transverse section, framed with narrow border rim. Sculpture: flat, dense tubercles, becoming elongated across anterior face of glabella and on anterolateral border; backwardly facing scaly tubercles on occipital ring, posterior border smooth. Surface of palpebral area and occipital ring markedly pitted, less obvious elsewhere. Postvincular doublure with wavy, short terrace ridges. Hypostome long semi-ellipsoid with straight hypostomal suture and narrow posterolateral border bearing three short spines at the posterior margin. Middle body is moderately vaulted; middle furrow very shallow, transverse; posterior lobe of middle body indistinct. Sculpture consists of thin tiny terrace ridges on anterior middle body and adaxial anterior wings. Thoracic segments without lateral axial lobes. Sculpture of axis with backwardly-facing, drop-like tubercles. Pygidium transverse, short (length is 43% of width), with wide parabolic posterior outline. Projection of maximum width crosses the middle of fourth axial ring. Axis low, narrow (width = 26% of pygidial width), long (length = 85% of total pygidial length), defined by straight, distinct, weakly converging axial furrows, with nine straight axial rings besides triangular terminal piece. Inter-ring furrows straight, distinct, reaching axial furrows, the anterior two with indistinct pseudo-articulating half-rings. Terminal piece flat, merging with broad postaxial ridge that narrows backwards, almost extending to posterior edge of pygidium. Pleural region moderately vaulted. Distance between axial furrow and fulcrum is 60% of distance between fulcrum and distal end of facet. There are seven moderately vaulted pleural ribs separated by deep thin pleural furrows. Interpleural furrows weak to indistinct. Anterior bands of ribs carrying a row of tubercles are slightly higher and longer than posterior ones. Ribs and pleural furrows almost reaching lateral edge of pygidium. Exoskeleton of pygidium pitted, with flat tubercles throughout that are densely crowded on anterior axial rings, and aligned on posterior ones and on pleural ribs. Posterolateral edge framed with thin rim.

Remarks. – This taxon was first presented in the unpublished thesis by Feist (1977) under the designation *Phacops* (*Chotecops*?) *hermannicristatus* sp. nov., after the *hermanni-cristatus* Zone to which it was thought to belong. This name constitutes a *nomen nudum* as the new species remained hitherto unpublished. Detailed conodont research subsequently undertaken by the second author (G.K.) revealed the assignment of the horizon to the Lowermost *asymmetricus* Zone (= *norrisi* Zone) (Feist & Klapper 1985). To avoid confusion the new taxon is renamed here.

***Cronierella postera* sp. nov.**
Figure 4J–L

Holotype. – Cephalon UM-IP 872, La Serre, Frasnian Zone 6 (Fig. 4J).

Type horizon and locality. – Grey-brown calcilutite, Serre Formation, lower member (Feist 1985); La Serre hill, trench A bed 133, Frasnian Zone 6 (Feist & Klapper 1985).

Etymology. – *Posterus* [Lat.] = later, referring to the later occurrence as the type species.

Other material. – Paratypes: cephala UM-IP 873–874, pygidium UM-IP 875, all from type locality and horizon.

Diagnosis. – Frontal wall of glabella moderately elevated; intercalating ring with transverse, low median lobe distinctly separated from back of anterior glabella by continuous S1; pygidium long with slightly truncated posterior outline, projection of maximum width opposite to fifth axial ring, facet long, axis remaining distinctly distant from posterior edge.

Remarks. – In comparison with the type species, the anterior glabella is a little lower (height reaching 53% of length of its anterior lobe), the anterior border slightly inflated, anterolateral borders framed by a thin rim, glabellar furrows S2 and S3 conspicuously impressed in exoskeleton, S1 continuous, curving forward medially. The intercalating ring is subdivided by shallow depressions, median lobe slightly curved, of even length medially to distally, conspicuously inflated (sag., exsag.). Postvincular doublure is horizontal. Eye lobe does not reach anterolateral border furrow. Postocular genal field is more than half length (exsag.) of adjacent posterior border. Sculpture: circular, low, dense tubercles, becoming elongated across ventral third of anterior face of glabella; tubercle row on posterior border; postvincular doublure with thin, discontinuous terrace ridges. Pygidium long (length is 47% of width) of subhexagonal outline, slightly truncated posteriorly. Projection of maximum width crosses back of fifth axial ring. Axis comprising 82% of total pygidial length remains distinctly distant

from posterior edge of pygidium. Distance between axial furrow and fulcrum is 56% of distance between fulcrum and distal end of facet. Ribs and pleural furrows remain distant from lateral edge of pygidium. Exoskeleton of pygidium with scarce small tubercles, slightly increasing in size on axial rings.

***Cronierella expansa* sp. nov.**
Figure 4M, N

Holotype. – Cephalon UM-IP 876, La Serre, Montagne Noire, Frasnian Zone 6 (Fig. 4M).

Type horizon and locality. – Grey-brown calcilutite, Serre Formation, lower member (Feist 1985); La Serre hill, trench A bed 129, Frasnian Zone 6 (Feist & Klapper 1985).

Etymology. – Expansus [Lat.] = expansive, referring to the transversely enlarged cephalon.

Other material. – Paratype: pygidium UM-IP 877 from trench A'42, equivalent level to type horizon; additional material: pygidium UM-IP 878, from A'42.

Diagnosis. – Cephalon wide, slightly longer than half width, S1 interrupted medially, median lobe of intercalating ring merging with anterior glabellar lobe. Pygidium long hexagonal with maximum width opposite sixth axial ring; axial furrow outwardly bowed on anterior two segments; axis hypobolic in outline posteriorly; eight axial rings with obvious pseudo-articulating half rings on anterior few; pleural field with six vaulted pleural ribs.

Remarks. – The new species is distinct by the wide parabolic outline of its cephalon that is a little longer than half width (54% of width) and the degree of glabella divergence (66°). It shares with *Cronierella postera* the height of the glabella and the slightly impressed S2 and S3 furrows. Distinct features of the intercalating ring comprise the straight uninflated median lobe that merges with the back of the anterior glabellar lobe and the trapezoidal, low lateral lobes. Librigenal subocular area is unswollen, posterior branch of suture indistinct. The pygidium, of similar length as that of *postera*, has a subhexagonal outline and is markedly truncated posteriorly. Projection of maximum width crosses back of fifth axial ring. The axis with broad hypobolic posterior outline, is as short as in *postera* (length = 82% of total pygidial length), remaining distinctly distant from posterior edge of pygidium. Particular features concern the axial furrows that are steadily outwardly curved adjacent to rings in anterior half of axis, converging uniformly thereafter. Three anterior axial rings exhibit distinct pseudo-articulating half rings. Axial furrow are interrupted medially behind terminal piece by thin, prominent postaxial ridge that fades away half way to posterior edge of pygidium. There are six vaulted pleural ribs separated by distinctly deep pleural furrows. Ribs and pleural furrows do not extend to lateral edge of pygidium. Exoskeleton of pygidium is smooth except for scarce tubercles on anterior pleural ribs and median axial rings.

***Cronierella*? sp. nov. A**
Figure 4C

Remarks. – A single cephalon (UM-IP 861) in light grey stylioline biomicrites of Upper *disparilis* Zone age was found on the eastern slope of Mont Peyroux hill near Col des Tribes (locality 7, CT-S section, bed 50 with *Polygnathus cristatus* and *P. dengleri*). The outline of the cephalon and glabella, and in particular the disposition of the intercalating ring and the occipital lobe, resemble traits of *Eldredgeops*. However, the palpebral area is much narrower (tr.), the palpebral furrow well discernible, the eye shorter, remaining farther from the posterior border furrow, and is lower with fewer lens rows (17) and lenses (a maximum of five in a row). In these features the taxon is very close to *Cronierella*, with the exception of the higher number of lenses that protrude from the scleral surface. We tentatively assign this taxon to *Cronierella*; its definite attribution is hindered by the currently missing pygidium. Awaiting additional material, we leave this taxon unnamed but consider it to be a new species.

Genus *Acutiphacops* gen. nov.

Type species. – *Acutiphacops medius* sp. nov.

Etymology. – After the acute anterior outline of cephalon.

Diagnosis. – Cephalon of narrow parabolic outline; almost flat-topped, pentagonal pre-occipital glabella with long anterior portion overhanging anterior border; short, cylindrical, protruding previncular doublure, edges of vincular furrow of similar elevation, long postvincular doublure; anteriorly situated high eyes with 12 rows of maximum four lenses; pygidium transverse, short, with moderately high axis remaining distant from posterior margin, 5–6 axial rings besides end-piece.

Remarks. – The new genus regroups taxa combining features that characterise *Acuticryphops* (anteriorly pointed, overhanging glabella, transverse pygidium with short axis) and, on the other hand, *Phacops* (facial suture running in deep border furrow, discrete cylindrical border, long postvincular doublure, visual surface considerably higher in front than to the rear). Notably, the pygidium is

very close to that of *Acuticryphops*. The new genus might represent the direct ancestor of *Acuticryphops.*

Occurrence. – Frasnian Zones 8–10, Montagne Noire (France), Tafilalt (Morocco).

Species included. – *Acutiphacops medius* sp. nov., Frasnian Zone 8, La Serre, Montagne Noire, France; *A. erfoudensis* (Richter & Richter, 1943), Late Devonian undetermined, *A. tchrafinensis* sp. nov., both Tafilalt, Morocco.

***Acutiphacops medius* sp. nov.**
Figure 5D–G

Holotype. – Cephalon UM-IP 883, La Serre, Montagne Noire, Frasnian Zone 8 (Fig. 5D).

Type horizon and locality. – Coarse light-grey crinoidal calcirudite, section La Serre A' bed 71 (Klapper 1989, pl. 2, fig. 10; Feist 2002, fig. 30b).

Etymology. – Medius [Lat.] = in between (*Phacops* and *Acuticryphops*).

Other material. – Paratypes: cephala UM-IP 884–885, pygidia UM-IP 886–887, all from type horizon and locality; additional material: four cephala UM-IP 888–891, two pygidia UM-IP 892–893 from type horizon and locality.

Diagnosis. – Cephalon with strongly diverging axial furrows; glabella with marked anterior overhang; anterior border furrow deep, anterior border narrow cylindrical, protruding, post-vincular doublure long; eye lobe three times longer than postocular genal field, encroaching onto anterolateral border for 75% of its length; pygidium transverse, truncated behind, five axial rings with sigmoidal inter-ring furrows, posterolateral margins without border.

Description. – Cephalon long (length 62% of width), of narrow parabolic outline. Anterior glabellar lobe is pentagonal, with obtusely pointed anterior contour, of very low, weakly vaulted lateral and transverse profiles, anteriorly a little higher than half length, with strong anterior overhang. Length is 74% of width. Portion anterior to maximum width is 48% of posterior portion. Axial furrows diverge at 84°; they are straight behind before their inward deviation by slight impingement of adaxial eye lobe on anterior glabella shortly behind inwardly-curved, bluntly-rounded glabellar corners. S1 slightly convex forward, shallow medially; S2 are ovoid depressions; S3 very week. Intercalating ring is narrow (tr.) (31% of cephalic and 49% of maximum glabellar width), tripartite, with band-like median lobe and well defined circular, slightly inflated and backwardly extending lateral lobes. Occipital ring twice as long as intercalating ring (sag.), extending forwards medially, without lateral lobes. Eye lobe is prominent, three times longer (exsag.) than distance between eye lobe and posterior border furrow, encroaching on to anterolateral border. Palpebral lobe wide (tr.), slightly inclined adaxially, with palpebral rim. Palpebral furrow deep, slightly convex outwards, visual surface kidney-shaped, moderately inclined abaxially, with 12 rows of lenses with a maximum of four in a row. Genal field gently vaulted. Facial suture meets subocular groove at the junction with lateral border furrow. Posterior and lateral border furrows rather deep, of even depth and mergeing with each other in obtuse angle. Anterolateral border furrow deviated by forward extension of eye lobe. Anterior border furrow deep. Anterior border is narrow cylindrical, rim-like, extending along edges of gently vaulted anterolateral borders.Vincular furrow deep, short (sag.), of circular curvature. Edges of vincular furrow are at same level. Postvincular doublure long (sag.), flat, densely covered with tiny short terrace ridges. Sculpture: entire surface of cephalon is densely covered with tubercles. Pygidium short (length = 43% of width) with angular anterolateral margins. Anterior edge between axial furrow and fulcrum is half as long as anterolateral edge. Posterior outline is straight or slightly embayed medially. Axis robust, high anteriorly, of moderate transverse vault behind, slightly curved in lateral profile with posterior end slightly elevated above postaxial field, wide (31% of pygidial width), short (77% of pygidial length), defined by deep, straight weakly tapering axial furrows that only partly surround the broadly rounded posterior end of axis, being interrupted medially by a short, weak postaxial ridge. There are five straight axial rings besides end piece. The two anterior rings exhibit small pseudo-articulating half-rings. First two inter-ring furrows reach axial furrows. Posterior inter-ring furrows slightly forwardly curved medially. Pleural field horizontal adaxially, rapidly downcurved abaxially, carrying five moderately elevated, almost straight ribs that are well defined by deep pleural furrows dying out well before reaching posterior margin, leaving a broad, uninflated border region. Surface of pygidium with spaced granules on axial rings and ribs.

***Acutiphacops erfoudensis* (Richter & Richter, 1943)**

1943 *Phacops* (*Phacops*) *erfoudensis* n. sp.; Richter & Richter, pp. 131–133, pl. 1, fig. 4.
1977 *Phacops* (*Chotecops*?) *erfoudensis*. – Chlupáč, p. 50.

Remarks. – Richter & Richter described rather fragmentary phacopid material found by Termier (1936) in a loose rock

sample with Late Devonian ammonoids in the region of Erfoud (SE Morocco). Despite the incompleteness of the trilobite remains and the uncertainty of both locality and age, they assigned the material to the new species *Phacops erfoudensis*, assuming a late Upper Devonian age for it as they considered its affinities to be with *Phacops granulatus* (Münster, 1840) and allies. Different characters, in particular the pentagonal outline and overhang of the anterior glabellar lobe along with the encroachment of the eye lobe onto the glabella adaxially are typical of the new genus, to which *erfoudensis* is assigned here. As it is most closely related to *Acutiphacops tchrafinensis* sp. nov. of mid-Frasnian age we assume a similar age for *erfoudensis*.

***Acutiphacops tchrafinensis* sp. nov.**
Figure 5A–C

Holotype. – Cephalon UM-IP 879, Bou Tchrafine, Tafilalt, Morocco, Frasnian Zone 10 (Fig. 5A).

Type horizon and locality. – Grey marly calcilutite, section Bou Tchrafine W, bed N (Becker & House 2000, fig. 1).

Etymology. – After locality Bou Tchrafine south of Erfoud, Morocco.

Other material. – Paratypes: cephalon UM-IP 880, pygidium UM-IP881; additional material: cephalon UM-IP 882.

Diagnosis. – Cephalon with moderate divergence of axial furrows and moderate glabellar overhang; eye lobe twice as long as postocular genal field, subocular groove merging with lateral border furrow anteriorly well in front of junction of facial suture with border furrow; pygidium gently rounded posteriorly, with six straight axial rings and a slightly inflated border laterally and posteriorly.

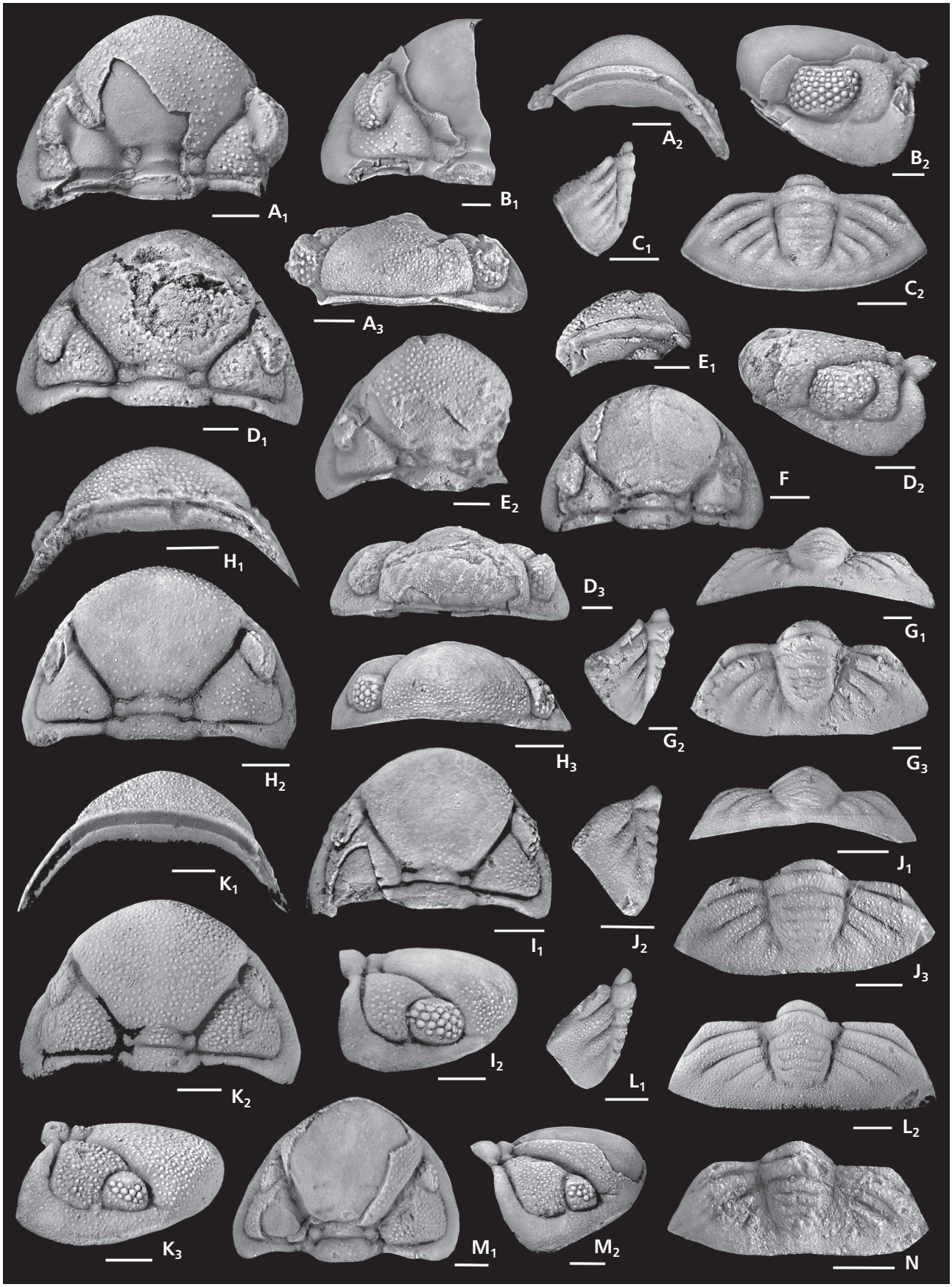
Remarks. – In comparison with the type species the new species has distinct features as follows. The cephalon is a little longer (length is 65% of width) and the anterior glabellar lobe, of which the length reaches 78% of its width, has only a slight anterior overhang. Axial furrows diverge at 67° and are inwardly deviated by marked encroachment of adaxial eye lobe on anterior glabella just behind angular corners of glabella. S1 transverse, slightly shallowing medially; S2 and S3 are discernible on internal mould. Intercalating ring is narrow (width = 34% of cephalic width), with narrow ridge-like median lobe and low, uninflated lateral lobes. Occipital ring short (sag.), as long as intercalating ring, scarcely extending forwards medially. Eye lobe is twice as long as distance between eye lobe and posterior border furrow, its anterior lower edge lying in the border furrow for a third of the length of the eye. Palpebral furrow deep, slightly convex outwards. Facial suture meets subocular groove at the posterior end of eye lobe, leaving a triangular strip of librigenal field between eye lobe and lateral border furrow. Sculpture consists of spaced, small drop-like tubercles on glabella and genal fields, lateral borders smooth. Anterior edge of pygidium between axial furrow and fulcrum is markedly shorter than length of anterolateral edge (64%). Posterior outline gently curved. Axis of moderate height, with sagittal profile merging behind with vaulted postaxial field, wide (28% of pygidial width), short (79% of pygidial length). There are six straight axial rings besides end-piece (which may contain relicts of two supplement axial rings). The second ring exhibits small pseudo-articulating half-ring. Pleural field moderately vaulted with four ribs and a slightly inflated border region. Posterior edge of pygidium framed by marked rim. Surface of pygidium is granulose with a few tiny tubercles on anterior axial rings and ribs.

The new species differs from its nearest relative *A. erfoudensis* by a longer eye-lobe with a higher number of lens rows, weaker divergence of axial furrows, lesser density of tuberculation and an un-crested posterior axis of pygidium. A closely related fragmentary cephalon was recovered from Frasnian Zone 10 of the Bou Tchrafine section by Helling & Becker (2012). A digital photograph of it, provided by S. Helling, reveals a very fine and dense granular sculpture unlike that of *tchrafinensis*; it might belong to a different probably new species.

Genus *Acuticryphops* Crônier & Feist, 2000

Type species. – *Trimerocephalus acuticeps* Kayser, 1889; Adorf, Rhenish Slate Mountains, Late Frasnian.

Figure 5. Specimens from Montagne Noire, France, except in A–C, M, N. • A–C – *Acutiphacops tchrafinensis* sp. nov., Bou Tchrafine, Tafilalt, Morocco; A – holotype cephalon UM-IP 879, dorsal (A_1), ventral (A_2), anterior (A_3) views; B – fragment of cephalon UM-IP 880, dorsal (B_1), lateral (B_2) views; C – pygidium UM-IP 881, lateral (C_1), dorsal (C_2) views. • D–G – *Acutiphacops medius* sp. nov., La Serre; D – holotype cephalon UM-IP 883, dorsal (D_1), lateral (D_2), anterior (D_3) views; E –cephalon UM-IP 884, partly exfoliated, ventral (E_1), dorsal (E_2) views; F – cephalon UM-IP 885, dorsal view; G – pygidium UM-IP 886, posterior (G_1), lateral (G_2), dorsal (G_3) views. • H–J – *Acuticryphops prorotundus* sp. nov.; H – holotype cephalon UM-IP 894 from Combe Rolland, ventral (H_1), dorsal (H_2), anterior (H_3) views; I – cephalon UM-IP 896 from La Serre, dorsal (I_1), lateral (I_2) views; J – pygidium UM-IP 895 from Combe Rolland, anterior (J_1), lateral (J_2), dorsal (J_3) views. • K–N – *Acuticryphops acuticeps*, K–L from Coumiac, M–N from Kahlleite Quarry, Thuringia, Germany; K – cephalon UM-IP 900, early form, ventral (K_1), dorsal (K_2), lateral (K_3) views; L – pygidium UM-IP 901, early form, lateral (L_1), dorsal (L_2) views; M – cephalon UM-IP 902, dorsal (M_1), lateral (N_2) views; N – pygidium UM-IP 903, dorsal view. Scale = 1mm.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Diagnosis (emended). – Cephalon with inverted lens-shaped previncular doublure merging with overhanging anterior glabella, continuously deep vincular furrow, narrow postvincular doublure; anterior outline of glabella rounded to obtusely pointed; eye lobe small, ovoid, as high in front as to the rear in anterolateral view, encroaching onto anterolateral border, palpebral furrows straight and diverging forward to slightly concave abaxially, merging with subocular groove in continuous curvature and depth, visual surface variably kidney shaped to oval with one to 23 lenses. Pygidium transverse, short, with low axis carrying five rings besides short end piece that does not reach posterior margin.

Species included. – *Acuticryphops acuticeps* (Kayser, 1889), Frasnian Zones 12–13, Rhenish and Thuringian Slate Mountains, Harz, England, Moravia, Montagne Noire, Hercynian Meseta of Morocco, NW Algerian Sahara, Canning Basin of Western Australia; *A. klapperi* Feist *et al.*, 2009, Frasnian Zone 13, Canning Basin, Western Australia; *A. prorotundus* sp. nov., Frasnian Zone 13, Montagne Noire.

Occurrence. – Western and Central Europe, North Africa, Western Australia.

Acuticryphops prorotundus sp. nov.
Figure 5H–J

1993 *Nephranops* sp. – Becker, p. 66.

Holotype. – Cephalon UM-IP 894, Combe Rolland, Montagne Noire, Frasnian Zone 13 (Fig. 5H).

Type horizon and locality. – Dark brown calcilutite, Combe Rolland road section at 2 m below top, SW of Vailhan village.

Other material. – Paratypes: pygidium UM-IP 895 from type horizon; cephalon UM-IP 896 from La Serre section C, bed 13, Frasnian Zone 13 (Klapper *in* Feist 1990, fig. 28); additional material: three cephala and two pygidia from type horizon and locality (UM-IP 897); 13 cephala, a thoracic segment and three pygidia from La Serre C, bed 13 (UM-IP 898); four cephala and three pygidia from Soureillé d'Izarne SW of Cabrières (UM-IP 899).

Etymology. – *Prorotundus* [Lat.] = rounded in front.

Diagnosis. – Cephalon of evenly rounded contour with bluntly curved glabellar corners, straight divergent palpebral furrows, long, flat palpebral lobes, ovoid eyes distant from posterior border furrow by three quarters of their length, lens-shaped palpebral lobes, kidney-shaped visual field with at least 18 lenses. Pygidium with wide axis of parabolic posterior contour, straight inter-ring furrows.

Description. – Cephalon markedly longer than wide (length/width ratio = 0.64), evenly rounded in outline, of moderate transverse vault. Anterior glabellar lobe has a rounded anterior contour, and is continuously high-vaulted transversely, less so in lateral profile except in front, where it is high (height in front of eye reaches 60% of length (sag.) of anterior glabellar lobe), strongly down-curved with marked anterior overhang. Axial furrows straight and diverging at 82° between S1 and junction with palpebral furrow, slightly curving inwards in front to form bluntly rounded glabellar corners. S1 furrow is slightly convex forward, shallow medially; S2 rather weak, unimpressed. Intercalating ring is narrow (tr.) (29% of cephalic and 46% of glabellar width), vaguely tripartite, with band-like, uninflated median lobe and poorly differentiated, low, small lateral lobes not extending backward. Occipital furrow slightlycurved forwards medially in parallel with S1, gently set back behind lateral lobes of intercalating ring. Occipital ring short, less than twice length of intercalating ring (sag.), scarcely extending forwards medially, notched anterolaterally and diminishing in length distally (exsag.), with weakly differentiated lateral lobes. Genal field evenly vaulted. Eye is ovoid in anterolateral view, surrounded by deep palpebral and subocular furrows, encroaching far onto anterolateral border. Distance between posterior border and eye is 79% of eye length (exsag.). Palpebral furrows straight, divergent. Palpebral lobes lens-shaped, long (exsag.), flat, bare, rearwards inclined, without palpebral rim. Visual surface is kidney shaped with palpebral suture dorsally concave in lateral view, as high in front as to the rear. There are between 18 and 23 lenses irregularly and densely arranged, markedly protruding above reduced sclera. Posterior facial suture runs on tiny triangular bridge interrupting lateral border furrow. Posterior and lateral border furrows merging in a uniformaly deep, parabolic curve. Borders slightly vaulted, widest opposite obtusely rounded genal angle. Anterolateral border narrowing adaxially to merge with inverted, crescent shaped previncular doublure. Vincular furrow deep throughout, scarcely curved medially. Postvincular doublure twice as long (sag.) as vincular furrow. Sculpture: tiny tubercles that are dense on anterior face of glabella, elsewhere widely spaced, tending to vanish on medial part of anterior glabella; palpebral lobes, lateral lobes of intercalating ring, posterior and lateral borders and postvincular doublure smooth. Pygidium transversely subrectangular (length/width ratio = 0.38) with curved, medially slightly transverse posterior outline. Axis is low, very wide (one-third of pygidial width), with five flat axial rings besides end piece, the first ring more

strongly vaulted, the second with pseudo-articulating half-ring. Inter-ring furrows straight, shallowing medially, do not reach axial furrows except first one. Axial furrows weakly tapering anteriorly, more strongly behind third ring, vanishing without postaxial closure distant from posterior edge of pygidium. End piece of axis extends rearwards, where it is slightly swollen, narrows, and almost reaches posterior edge. Pleural field slightly vaulted, with four poorly vaulted pleural ribs, defined by deeply marked pleural furrows. Interpleural furrows are discernible. Ribs and furrows remain far from posterolateral borders. Sculpture: medium-sized tubercles throughout.

Remarks. – The new species is close to early morphs of *Acuticryphops acuticeps*. The main differences in the former are the outline of the anterior glabellar lobe which is not pentagonal as a result of the inward curvature of the axial furrows anteriorly; the palpebral lobes are markedly wider; and the eye is much longer with a kidney-shaped (instead of oval) visual surface having more lenses. In addition, the pygidium has a much broader axis with straight inter-ring furrows. Specimens from locality La Serre C bed 13 were eronously assigned to *Nephranops* by Feist (*in* Becker 1993, p. 66).

***Acuticryphops acuticeps* (Kayser, 1889)**
Figure 5K–N

2009 *Acuticryphops acuticeps*. – Feist *et al.*, pp. 24–27, fig. 5a–q (earlier synonymies herein).
2016 *Acuticryphops acuticeps*. – McNamara & Feist, p. 257, figs 2, 3.

Material. – Cephalon UM-IP 900, pygidium UM-IP 901, early form, Coumiac Upper Quarry bed 21, Frasnian Zone 12; cephalon UM-IP 902, pygidium UM-IP 903, Kahlleite Quarry, Thuringia, Frasnian Zone 12.

Remarks. – Acuticryphops acuticeps is the most common and widely distributed phacopid species in Frasnian sections prior to its extinction at the base of the Upper Kellwasser horizon. Outstanding evidence of intraspecific variation in the number of eye lenses of the visual surface was analysed in successive populations of the Coumiac section by Feist (1991), Feist & Schindler (1994) and Crônier *et al.* (2004). During the existence of the taxon trends related to eye reduction concern the outline and position of the eye lobe that reduces in size from behind to a small, subtriangular bulbous lobe. Reduction of eye lens numbers is concomitant with continuous transformation of the outline of the visual surface from an initial kidney-shaped pattern to an oval one where the palpebral lobe is triangular and the palpebral suture is dorsally convex in anterolateral view ("*cryptophthalmus* pattern" of Richter & Richter 1926). Early morphs such as those presented here (Fig. 4L) have a kidney-shaped visual surface with 14 or more lenses. In addition to the variation in features of the eye lobe, populations of early morphs vary in the degree of curvature of the anterior glabellar outline, and in the length and degree of curvature of the postvincular doublure.

Genus *Occitanella* gen. nov

Type species. – *Occitanella hexagonalis* sp. nov.

Etymology. – After *Occitania*, Roman province in southern Gaul.

Diagnosis. – Cephalon with moderately vaulted glabella without anterior overhang, small forwardly placed eyes not reaching anterolateral border furrow, long and shallow vincular furrow with low inflated posterior edge, markedly convex postvincular doublure; hypostome with conspicuously continuous median furrow and inflated posterior lobe. Pygidium long, with short, narrow axis, long postaxial ridge and postaxial field.

Remarks. – We assign the Australian taxon *Trimerocephaloides*? *linguiformis* Feist *et al.*, 2009 to the new genus *Occitanella* with question on account of the considerable length of the pygidium with rather short axis prolonged by an extended postaxial ridge, characters that are as such only known in *Occitanella*. However the new assignment must be reconsidered when cephalic characters of *linguiformis* become available.

Occurrence. – Early Frasnian zones 3 and 4 (Montagne Noire), Zone 11? (Canning Basin, NW Australia).

Species included. – *Occitanella hexagonalis* sp. nov., Frasnian Zone 3, Pic de Bissous, Montagne Noire; *O. postinflexa* sp. nov., Col du Puech de la Suque, Frasnian Zone 4, Montagne Noire. Assigned with question: *O.*? *linguiformis* (Feist *et al.*, 2009), Frasnian Zone 11, Canning Basin, NW Australia; *O.*? sp. Frasnian Zone 4, Mont Peyroux, Montagne Noire.

***Occitanella hexagonalis* sp. nov.**
Figure 6A–C

Holotype. – Pygidium UM-IP 904, Pic de Bissous, Montagne Noire, Frasnian Zone 3 (Fig. 6B).

Type horizon and locality. – Brick-red calcilutite, section VS-E, bed 49 (Feist 1983, fig. 13; Klapper 1985, fig. 1), southern steep face of Pic de Bissous.

Etymology. – *Hexagonalis* [Lat.], after the outline of the pygidium.

Other material. – Paratypes: cephala UM-IP 905–906; additional material: four cephala UM-IP 908 and two pygidia UM-IP 909; all from type locality and horizon.

Diagnosis. – Cephalon with narrowly parabolic anterior outline, anterior axial furrows inwardly curved around glabella corners, marked palpebral rim; pygidium hexagonal with high axis, prominent first axial ring, curved pleural ribs, inconspicuously rounded lateral and posterior margins with slightly embayed posterior edge.

Description. – Cephalon long (length = 64% of width) with parabolic anterior outline. Anterior glabellar lobe bulbous, slightly pointed in front, long (76% of cephalic length), of high transverse vault, moderately vaulted in lateral profile, vertically sloping anteriorly without overhang. Anterior border thick, rounded in sagittal profile, protruding. Axial furrows anterior to intercalating ring are straight, diverging at 66° until eye lobe, curving inwards around frontal glabellar lobe. S1 straight, shallowing medially, S2 and S3 indiscernible. Width (tr.) of intercalating ring is 56% of anterior glabellar width and one-third of cephalic width, is indistinctly tripartite: median lobe elongated, prominent, poorly separated from low lateral lobes. Occipital furrow deep, straight. Occipital ring is of moderate length (sag.), twice that of median intercalating ring, moderately vaulted (sag.), without lateral lobes. Eye short (distance between visual surface and posterior border furrow = 70% of eye-length), reaching anterolateral border furrow. Visual surface kidney shaped, strongly sloping abaxially, distinctly vaulted dorsoventrally, with 11 vertical rows of lenses with a maximum of four per row (35 lenses in total). Palpebral lobes are crescent shaped, framed by thick palpebral rim. Palpebral furrows are distinct, continuous, diverging forward and almost straight. Posterior and lateral border furrows continuously deep and merging with each other in an obtuse angle. Vincular furrow is very wide (sag.) and shallow, with medially rounded, low posterior edge. Postvincular doublure is twice as long as vincular furrow (sag.), inflated medially, with slightly curved hypostomal suture. Sculpture consists of coarse granules throughout, finer on borders. Postvincular doublure is densely covered with thin discontinuous terrace ridges.

Pygidium is distinctly long (length/width ratio = 61%), with pronounced hexagonal outline and long anterolateral contour. Anterior margin is distinctly shorter (tr.) than anterolateral margin (64%). Posterior margin is narrow (tr.), slightly embayed medially. Projection of maximum pygidial width crosses sixth axial ring. Axis is narrow (29% of pygidial width), strongly convex across first ring, distinctly subdued thereafter, short (65% of pygidial length). Axial furrows converge in a straight line except around end piece of axis where they converge more strongly and are interrupted by postaxial ridge. There are six–seven axial rings (besides end-piece), the first one higher and distinctly longer (sag.), the last ones poorly defined. Inter-ring furrows straight, wide (sag.) and shallow, not reaching axial furrows, except anterior two that are deeper and curve backwards distally. End piece is triangular, low, merging medially with distinct postaxial ridge that dies out mid-way to posterior edge of pygidium. Pleural field is wide, horizontal adaxially, strongly downcurved distally, with six ribs whose posterior bands are distinctly elevated, forming slightly backwardly curved crests that almost reach posterolateral margins. First pleural furrows markedly incised, remainder much shallower. Lateral and posterior margins with almost inconspicuously swollen border. Exoskeleton of pygidium is granulose.

Occitanella postinflexa sp. nov.
Figure 6D–K

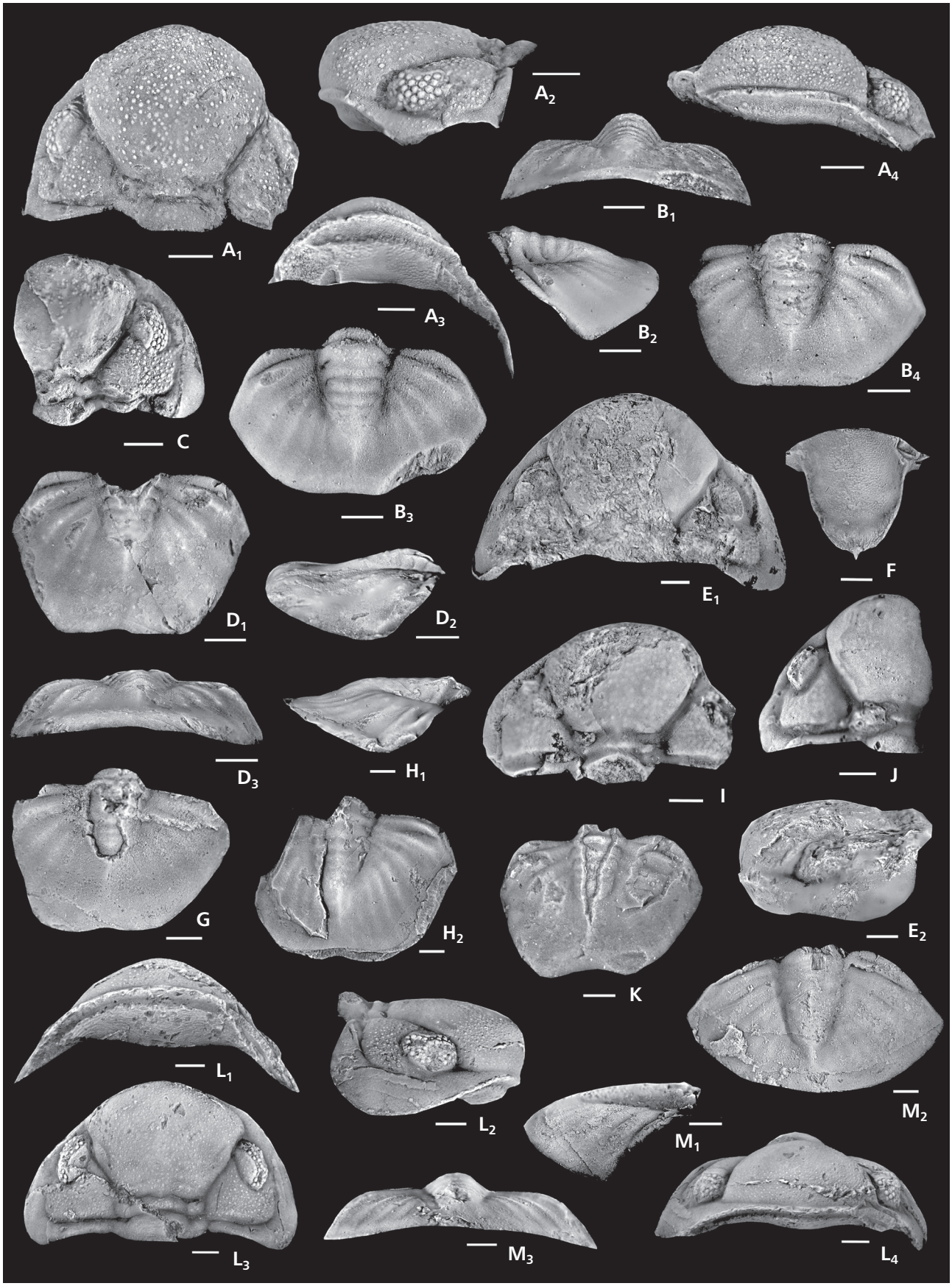
Holotype. – Pygidium UM-IP 910, Col du Puech de la Suque, Montagne Noire, Frasnian Zone 4 (Fig. 6D).

Type horizon and locality. – Grey-brown calcilutite with *Erbenicoryphe nazairensis* Feist, 2003, section CPS-E, bed 58 (Feist & Klapper 1985, fig. 5)

Etymology. – *Postinflexus* [Lat.] = embayed behind.

Other material. – Paratypes: cephala UM-IP 911–913, hypostome UM-IP 914, pygidia UM-IP 915–917; additional material: eight cephala UM-IP 918, four pygidia UM-IP 919.

Figure 6. All specimens from Montagne Noire, France. • A–C – *Occitanella hexagonalis* sp. nov., Pic de Bissous; A – cephalon UM-IP 905, dorsal (A_1), lateral (A_2), ventral (A_3), anterior (A_4) views; B – holotype pygidium UM-IP 904, posterior (B_1), lateral (B_2), dorsal (B_3), dorsal (latex cast of external mould, B_4) views; C – fragmentary cephalon UM-IP 906, dorsal view. • D–K – *Occitanella postinflexa* sp. nov., Col du Puech de la Suque; D – holotype pygidium UM-IP 910, dorsal (D_1), lateral (D_2), posterior (D_3) views; E – cephalon UM-IP 911, dorsal (E_1), lateral (E_2) views; F – hypostome UM-IP 914, ventral view; G – pygidium UM-IP 915, dorsal view; H – pygidium UM-IP 916, lateral (H_1), dorsal (H_2) views; I – exfoliated cephalon UM-IP 912, dorsal view; J – fragmentary cephalon UM-IP 913, latex cast of external mould, dorsal view; K – pygidium UM-IP 917, dorsal view. • L, M – *Occitanella*? sp., Mont Peyroux; L – cephalon UM-IP 921, ventral (L_1), lateral (L_2), dorsal (L_3), anterior (L_4) views; M – pygidium UM-IP 920, lateral (M_1), dorsal (M_2), posterior (M_3) views. Scale = 1mm.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L4

Diagnosis. – Cephalon with gently curved anterior outline, obtusely angled corners of anterior glabellar lobe. Pygidium elongated subtrapezoidal with very short axis, distally straight posterior ribs, wide inflated posterior and postero-lateral border, pronounced embayment of posterior margin.

Remarks. – In comparison with the type species the new species has the following distinct features: the cephalon is wider (length = 55% of width) with gently rounded anterior outline, and an anterior glabellar lobe with a parabolic anterior contour, the axial furrows are less diverging (at 60°) until meeting border furrow, where they define the angular corners of glabella. Visual surface of eye lobe is inflated, sloping moderately abaxially, and its distance from posterior border almost equals eye length. Palpebral lobes are without palpebral rim, flat, palpebral furrows very slightly adaxially convex in curvature. Post-vincular doublure is three times longer than vincular furrow, with broadly rounded anterior margin (sag.), flat posteriorly. Hypostome (unknown in the type species) is a little longer than wide (without wings) with gently curved hypostomal suture and narrow lateral borders flattening posteriorly. Posterior margin with obvious median spine; additional spines are not evident. Middle body highly vaulted. Middle furrow is distinct, wide, of moderate depth, deepening distally, forming transverse parabolic depression. Posterior lobe of middle body distinctly inflated as far as posterior margin. Sculpture consists of tiny, sometimes fused granules, arranged in backwardly-convex rows. Pygidium is very long (length/width ratio = 69%), with pronounced trapezoidal outline and short anterolateral contour. Pleural margin adaxial to fulcrum approximates length of anterolateral margin. Posterolateral margins straight and converging, very long. Posterior margin as long as posterolateral margin, sigmoidal with pronounced median embayment. Projection of maximum pygidial width crosses fifth axial ring. Axis is very short (sag.), slightly longer than distance between axis and posterior edge of embayment, merging behind with rather long, prominent, thin postaxial ridge. Transverse profile of axis is very low except for first axial ring which is higher than the others. Pleural field with six ribs; posterior pleural bands are thin and distinctly elevated, the first two anterior curved slightly backwards, the remainder straight. Posterolateral and posterior margins with weakly swollen, broad border separated from pleural field by shallow depression. Exoskeleton of pygidium is smooth; posterior pleural bands carry single rows of granules.

***Occitanella*? sp.**
Figure 6L, M

Remarks. – Single specimens of a well-preserved cephalon (UM-IP 921) and a pygidium (UM-IP 920) were found in dark-red biomicrites of bed CT-S 78 on the eastern slope of Mont Peyroux near Col des Tribes, Frasnian Zone 4 (with *Ancyrodella promosica*). Their co-occurrence in the same bed, their similar sculpture, and the absence of any other phacopid remains might indicate their conspecificity but this cannot be demonstrated without further material. Their generic assignment is also problematic as the cephalon shares traits of both *Occitanella* and *Chlupacops*. The cephalon resembles those of *Chlupacops* in the short, subtrapezoidal, anterolaterally slightly embayed glabella as well as in the deep and narrow vincular furrow. It is distinct mainly in the less advanced eye lobe, the blunt posterior edge of the vincular furrow and the inflated postvincular doublure, features that characterise *Occitanella*. By contrast, the pygidium found associated with the cephalon in the same bed differs clearly from *Chlupacops* in its extended length, the short, slender, posteriorly pointed axis with a long, prominent postaxial ridge, and a wide pleural field with 6 low ribs and faint pleural furrows. In these traits the pygidium is close to the type species of *Occitanella*. It is distinct by its evenly curved posterior outline and the faint axial rings and pleural ribs. Awaiting additional material, we leave this taxon unnamed and assign it with question to *Occitanella.*

Genus *Chlupacops* Feist, 2016 *in* Feist *et al.* (2016)

Type species. – *Chlupacops laticeps* Feist, 2016 *in* Feist *et al*. (2016). Marhouma, Saoura region, north-western Algerian Sahara, Frasnian Zone 5/6.

Diagnosis (emended). – Cephalon wide and short with gently rounded genal angles; glabella very wide anteriorly, with short anterior portion, low transversely, anterolaterally slightly embayed, with steep anterior wall not overhanging in front; sagittally short tripartite intercalating ring; small forwardly-positioned eye with reniform visual surface extending forwards to border furrow or slightly encroaching onto border; divergent, deep, almost straight palpebral furrows, narrow lens-shaped palpebral lobe; cylindrical previncular doublure forming protruding anterior border; continously deep vincular furrow, post-vincular doublure long to moderate in sagittal length. Pygidium of high lateral and transverse profile; axis high, with rounded posterior end not reaching posterior margin, with up to eight straight axial rings and deep axial furrows; pleural field with 4–5 vaulted ribs markedly defined by deep pleural furrows that remain distant from postero-lateral margin. Sculpture: dense small-grained tuberculation.

Remarks. – Numerous new taxa from the Montagne Noire exhibit a considerable degree of variability concerning in particular the size of the eye and its visual surface, the

Table 1. Measurements of ratio parameters, angle of divergence between cephalic axial furrows (corners of anterior glabella – S1), projection of maximum pygidial width in different species of *Chlupacops*.

Chlupacops	*laticeps*	*cryphoides*	aff. *cryphoides*	*angularis*	*clapassou-sensis*	*migrans*	*rectannu-latus*	*narbon-nensis*
cephalon								
length/width	0.5	0.63	0.62	0.56	0.55	0.55	0.55	0.63
glabella anterior to S1								
length/width	0.62	0.65	0.69	0.66	0.68	0.69	0.71	0.77
length ant. portion/length	0.45	0.42	0.42	0.41	0.42	0.39	0.4	0.41
width/cephalic width	0.59	0.63	0.62	0.63	0.63	0.59	0.6	0.62
angle of divergence	67°	67°	66°	63°	67°	61°	61°	62°
intercalating ring								
length (medially)/width	0.12	0.17	0.19	0.18	0.14	0.15	0.13	0.20
width/width glabella	0.51	0.49	0.53	0.5	0.54	0.56	0.53	0.52
width/width cephalon	0.31	0.33	0.33	0.33	0.34	0.35	0.32	0.32
visual surface								
number of lens rows	6–7		11	10	11	13	12	14
maximum lenses/row	3	4	4	4	4	4–5	4	5
postocular field								
length/eye-length	0.9	1.18	0.67	0.63	0.61	0.42	0.46	0.42
length/length + eye length	0.5	0.52	0.41	0.34	0.4	0.31	0.32	0.31
pygidium								
length/width	0.5		0.46		0.47	0.48	0.49	0.47
articulating/anterolat. edge	0.53		0.5		0.6	0.52	0.62	0.6
pyg. axis								
length/pygidial length	0.88		0.86		0.89	0.81	0.89	0.77
width/pygidial width	0.32		0.28		0.28	0.33	0.31	0.31
number of rings	7 + 1		7 + 1		8 + 1	7 + 1	7 + 1	7 + 1
maximum pygidial width	6th ring		6th ring		4th inter-ring furrow	end of axis	4th ring	6th ring

degree of its forward extend, the course of the palpebral furrow, generally straight divergent but in some cases slightly convex adaxially or abaxially, and the profile of the anterior face of the glabella which is more or less vaulted but without overhanging the anterior border. In comparison with the type species the new taxa have a shorter anteriormost glabella in front of its maximum width, longer eyes and longer (sag.) more prominent intercalating rings. The original diagnosis is herewith emended to take into account the variability of characters. Variability in the ratio of dimensions, parameters of glabella divergence, number of lens rows, lenses, pygidial axial rings and position of maximum pygidial width are listed in Table 1.

Feist *et al.* (2016) questionably assigned the Givetian taxa *Eocryphops*? *reichi* (Kegel, 1932) and *Chotecops*? *spectabilis* (Meischner, 1965) to *Chlupacops*. According to the emended diagnosis this assignment is no longer followed here. Indeed, unlike *reichi*, all representatives of *Chlupacops* have well developed tripartite intercalating rings and eyes reaching the anterolateral border or encroaching onto it. In addition, the visual surface in *Chlupacops* specimens are always reniform and composed of at least 15 lenses aligned in several vertical rows, whereas *reichi* has an elliptic visual surface with only eight lenses which recalls the configuration in *Eocryphops* as stated by Holloway (2005). The glabella of *spectabilis*, though similar in outline and profile to representatives of *Chlupacops*, is narrower (tr.) (56% of cephalic width vs 59%–63% in *Chlupacops*), whereas the pygidium has a longer and narrower, posteriorly pointed axis reaching the posterior margin, and more pleural ribs (six versus four). In these features *spectabilis* is closer to contemporaneous late *Chotecops* species such as *C. koeneni* (Holzapfel, 1895) rather than to species of *Chlupacops*.

Species included. – *Chlupacops laticeps* Feist *in* Feist *et al*., 2016, Marhouma, NW Algerian Sahara, Frasnian Zone 5/6; *Ch. cryphoides* (Richter & Richter, 1926), Sessacker, Rhenish Slate Mountain, FZ 12; *Ch.* aff. *cryphoides* (Richter & Richter, 1926) *sensu* Feist *et al.* (2016), Marhouma, NW Algerian Sahara, Frasnian Zones 8–10 undifferentiated; *Ch. angularis* sp. nov., Col du Puech de la Suque, Montagne Noire, middle? Frasnian

undifferentiated; *Ch. clapassousensis* sp. nov., Mont Peyroux, Montagne Noire, FZ 8–10 undifferentiated; *Ch. migrans* sp. nov., La Serre, Montagne Noire, FZ 6; *Ch. rectannulatus* sp. nov., La Serre, Montagne Noire, FZ 7; *Ch. narbonnensis* sp. nov., Col du Puech de la Suque, Montagne Noire, FZ 5; *Ch.* sp. (= *Chotecops* sp. *sensu* Helling & Becker 2012), Seheb-el-Rhassal, Tafilalt, Morocco, FZ 7 *C*; included with question: *Ch.*? *postaltaicus* Maximova, 1960 and *Ch.*? *pronini* Maximova, 1955 both from latest Frasnian of Rudny Altai and eastern slope of Urals respectively.

Occurrence. – Saoura region, north-western Algerian Sahara, Tafilalt (Morocco), Montagne Noire, Rhenish and Thuringian Slate Mountains.

***Chlupacops angularis* sp. nov.**
Figure 7A–C

Holotype. – Cephalon UM-IP 922, Col du Puech de la Suque, Montagne Noire, middle? Frasnian undifferentiated (Fig. 7A).

Type horizon and locality. – Isolated loose rock of light pink calcilutite in middle? Frasnian of Col du Puech de la Suque section CPS-E (Feist & Klapper 1985, fig. 5).

Etymology. – *Angularis* [Lat.] = angular, referring to angular bend of postvincular doublure.

Other material. – Paratypes: fragmentary cephala UM-IP 923–924; additional fragmentary cephalon with eye UM-IP 925a.

Diagnosis. – Cephalon with wide anterolaterally truncated outline, anteromedially prominent composite glabellar lobe with obtusely-angular lateral and traverse anterior profile and very high vertical anterior wall, straight slightly prominent intercalating ring, short occipital ring, vincular furrow bluntly curved medially, postvincular doublure triangular with medially obtusely-angular anterior outline.

Remarks. – The new taxon is only known from internal moulds of its cephalon and as such dimensions might be slightly different according to the external mould. Outline and most dimensions of cephalon and glabella fit diagnostic features of the genus. It is distinct from all other species of *Chlupacops* mainly by the prominent anterior glabella with very high and vertical anterior wall, forming an obtuse angle with dorsal vault of glabella in lateral view. Glabella bulges medially at junction between dorsal surface and steep anterior wall, and has, in ventral view, an obtusely angular transverse profile (Fig. 7B). In parallel, the anterior and posterior borders of the vincular furrow are bent medially to form obtuse angles without diminishing the length (sag., exsag.) of the vincular furrow. As a result, the postvincular doublure has a triangular outline, which is not seen in any other phacopid. Visual surface carries about 10 rows of lenses, with a maximum of four lenses in a row. Internal mould of exoskeleton exhibits a few spaced tubercles, relicts of external sculpture.

***Chlupacops clapassousensis* sp. nov.**
Figure 7D–F

1995 *Phacops* n. sp. a. – Feist, p. 236, fig. 11.6 (USTM-RF 116).

Holotype. – Cephalon UM-IP 925, Clapassous, Montagne Noire, Frasnian Zone 8–10 undifferentiated (Fig. 7D).

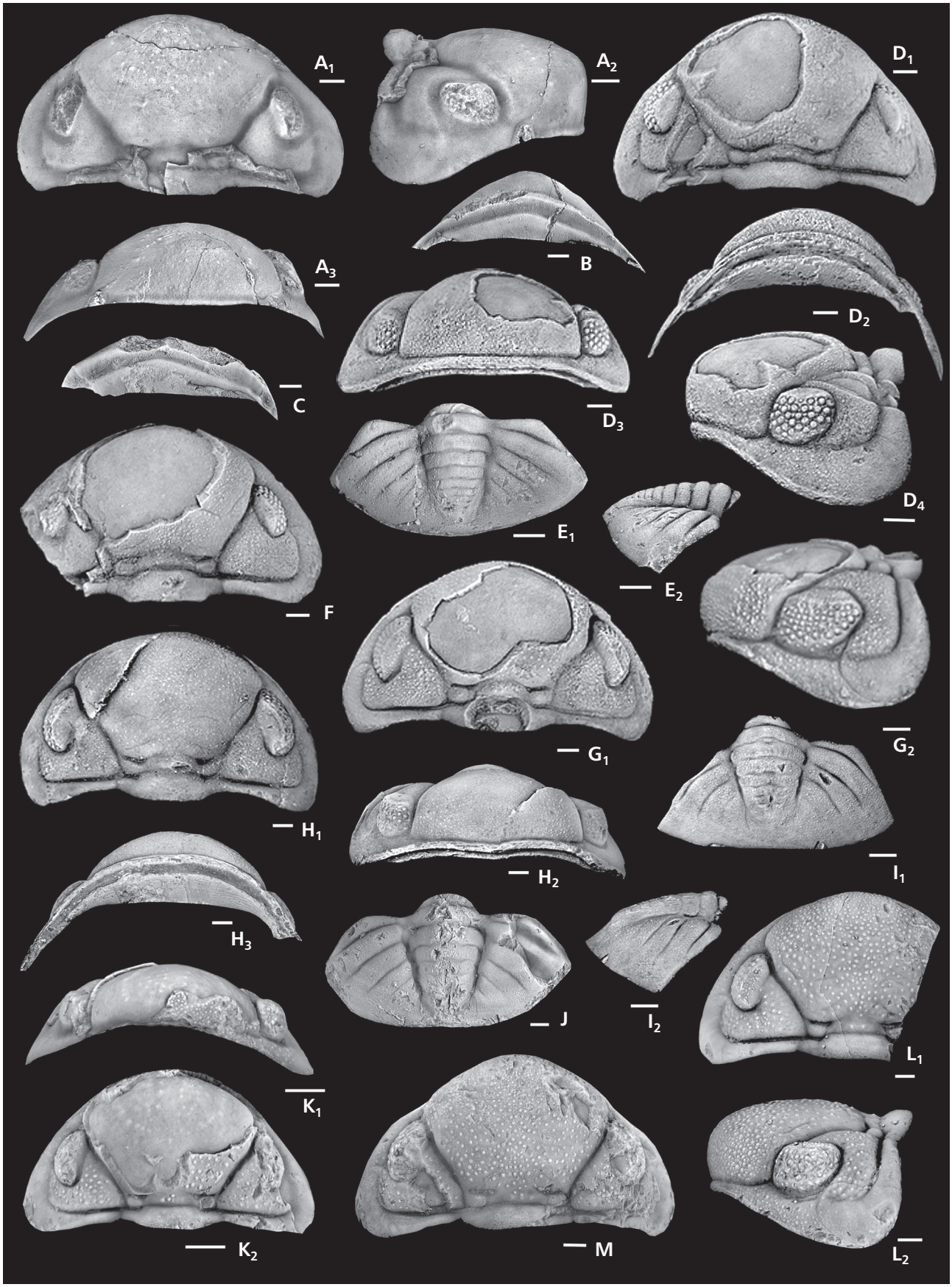
Type horizon and locality. – Brown, pink-stained calcilutite, Clapassous, western slope of Puech de la Suque hill, at 1.4 km SE of Saint-Nazaire-de-Ladarez.

Etymology. – After "Clapassous", western hill slope of Puech de la Suque.

Other material. – Paratypes: cephalon USTM-RF 116, pygidium UM-IP 926; additional material: six cephala and a pygidium UM-IP 927, all from type locality and horizon.

Diagnosis. – Glabella high-vaulted transversely with sigmoidal intercalating ring; small, horizontal palpebral lobes with straight palpebral furrows; pygidium transverse with parabolic posterior outline, axis long with eight axial rings, pleural field of moderate vault with 5 ribs,

Figure 7. All specimens from Montagne Noire, France. • A–C – *Chlupacops angularis* sp. nov., Col du Puech de la Suque; A – holotype, exfoliated cephalon UM-IP 922, dorsal (A_1), lateral (A_2), anterior (A_3) views; B – exfoliated fragmentary cephalon UM-IP 923, ventral view showing triangular postvincular doublure; C – exfoliated fragmentary cephalon UM-IP 924, ventral view showing triangular postvincular doublure. • D–F – *Chlupacops clapassousensis* sp. nov., Clapassous; D – holotype cephalon UM-IP 925, dorsal (D_1), ventral (D_2), anterior (D_3), lateral (D_4) views; E – pygidium UM-IP 926, dorsal (E_1), lateral (E_2) views; F – cephalon USTM-RF 116, dorsal view. • G–I – *Chlupacops migrans* sp. nov., La Serre; G – cephalon UM-IP 928, dorsal (G_1), lateral (G_2) views; H – holotype cephalon UM-IP 929, dorsal (H_1), anterior (H_2), ventral (H_3) views; I – pygidium UM-IP 930, dorsal (I_1), lateral (I_2) views. • J–M – *Chlupacops rectannulatus* sp. nov., La Serre; J – pygidium UM-IP 937, dorsal view; K – holotype cephalon UM-IP 934, anterior (K_1), dorsal (K_2) views; L – incomplete cephalon UM-IP 935, dorsal (L_1), lateral (L_2) views; M – cephalon UM-IP 936, dorsal view. Scale = 1mm.


A1
A2
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B
A3
D2
C
D3
D4
E1
E2
F
G1
G2
H1
H2
I1
H3
J
I2
L1
K1
K2
M
L2

pleural furrows straight, weak interpleural furrows on anterior ribs.

Remarks. – The new species shares the wide angle of divergence of cranidial axial furrows and the configuration of a small eye and lens-shaped palpebral lobes with *Ch. laticeps* and *cryphoides*. Comparatively the other species of the genus have a smaller angle of divergence, longer eyes and wider, slightly crescent-shaped palpebral lobes. The main features that characterise *clapassousensis* concerne the shape and dimensions of the intercalating ring. It is distinct from the other species by its sigmoidal outline; it is a little longer (sag.) than in *laticeps* and *rectannulatus* but markedly shorter than in the other species, hardly tripartite with slightly forwardly curved median lobe, poorly inflated and poorly separated from small trapezoidal lateral lobes. S1 is markedly sigmoidal, continously impressed, deeply abaxially, slightly shallower medially. Other particular cephalic features are as follows: Occipital ring twice length of intercalating ring (sag.), slightly flattened medially, notched behind apodemal pits defining hints of partial lateral occipital lobes. Facial suture poorly impressed, meeting subocular groove shortly behind the junction of the latter with border furrow. Postvincular doublure with blunt anterior edge, flat, a little higher than posterior edge of previncular doublure. The pygidium is close to the type species in overall shape. It is a little longer and has a shorter oblique anterolateral edge. The axis has more axial rings, the pleural field 4–5 weakly vaulted pleural ribs, the anterieurs with perceptible interpleural furrows. Sculpture: uniforme very dense fine granules throughout, a few tubercles on median lobe of intercalating ring, postvincular doublure with fine granules and wavy discontinuous terrace ridges.

***Chlupacops migrans* sp. nov.**
Figure 7G–I

partim 1977 *Phacops* (sg.?) *migrans* n. sp. – Feist, p. 179, pl. 16, fig. 8 (*nomen nudum*; *non* fig. 12 = *Chlupacops clapassousensis* sp. nov.).

Holotype. – Cephalon UM-IP 929, La Serre, Montagne Noire, Frasnian Zone 6 (Fig. 7H).

Type horizon and locality. – Grey-brown trilobite biomicrite, Serre Formation, lower member (Feist 1985); La Serre hill, trench A'48, Frasnian Zone 6 (Feist & Klapper 1985).

Etymology. – *migrans* [Lat.] = migrating, after the forward move of the eye.

Other material. – Paratypes: cephalon UM-IP 928, pygidium UM-IP 930; additional material: five cephala UM-IP 931, two pygidia UM-IP 932, all from type locality and horizon; cephalon UM-IP 933 from Clapassous.

Diagnosis. – Anterior glabella low and short anteriorly to maximum width, laterally embayed; axial furrows inward-curved; intercalating ring markedly tripartite with inflated lobes, median lobe ovoid, protruding; S1 curved forward and very shallow medially, long eye lobes; pygidium subtrapezoidal, truncated behind with very long anterolateral edge and backwardly positioned maximum width, wide and short axis, strongly backwardly curved pleural furrows.

Remarks. – The most distinctive trait of the cephalon is the sigmoidal course of the axial furrows. They are inwardly curved between S1 and the junction of the palpebral furrow, followed anteriorly by the embayment adaxially to the anterior end of the eye lobes before reaching the glabellar corners. These features undergo considerable variation within the population associated in the same bed. The sigmoidal curvature of the axial furrows is extreme in the figured specimen (Fig. 7G), whereas in other specimens of the same size, such as the holotype, the embayment, though present, is much less marked. Instability in the course of the palpebral furrows is also obvious. In most cases these are slightly curved but, as in the holotype, curved on the left side and straight on the right (Fig. 7H$_1$). Other particular features concern the intercalating ring and the eye-complex. S1 sigmoidal, deep and straight or slightly forwardly directed abaxially, much shallower and thinner medially. Intercalating ring is straight slightly forwards-enlarged medially, markedly tripartite, with inflated median lobe, elevated as high as base of anterior glabellar lobe in lateral view, separated from lower, inflated, subtriangular to subquadrangular lateral lobes. Occipital ring is evenly rounded in lateral profile, devoid of lateral occipital lobes. The eye lobe, similar to *narbonnensis*, has the longest extent (exsag.) among species of *Chlupacops*. Subocular groove deeply marked posteriorly, merges with anteriormost genal field before reaching anterolateral border furrow. Facial suture is impressed, meeting subocular groove adaxially far behind the junction of the latter with border furrow, defining a depressed triangular area on librigena between subocular groove and lateral border furrow. Sculpture: fine granules of various sizes throughout, postvincular doublure with wavy discontinuous rows of fused granules. The pygidium is dissimilar to the other species by its outline, the wider axis and the strong curvature of pleural furrows. The axis is moderately high, with posterior end slightly higher than postaxial region, remaining markedly distant from posterior edge. Axial furrows moderately converge backward, slightly less so behind second axial ring, fading away around posterior tip. Axial rings are

straight and low, inter-ring furrows slightly sigmoidal, shallow, the first four reaching axial furrows. Hints of pseudo-articulating half rings are perceptible on axial rings 2 to 4. Pleural region moderately and evenly vaulted with deep, backwardly curved pleural furrows that die out beyond inner two-thirds of pleural region. Weakly impressed interpleural furrows are discernible on anterior three ribs.

***Chlupacops rectannulatus* sp. nov.**
Figure 7J–M

Holotype. – Cephalon UM-IP 934, La Serre, Frasnian Zone 7 (Fig. 7K).

Type horizon and locality. – Light-grey trilobite biomicrite, Serre Formation, lower member (Feist 1985); La Serre hill, trench A'60, Frasnian Zone 7 (Feist & Klapper 1985; Klapper 1989, pl. 3, figs 3, 4).

Etymology. – Rectannulatus [Lat.] = with straight (intercalating) ring.

Other material. – Paratypes: cephala UM-IP 935–936, pygidium UM-IP 937; additional material: three cephala UM-IP 938, two pygidia UM-IP 939; all from type locality and horizon.

Diagnosis. – Cephalon gently vaulted transversely, with low anterior glabella, medially interrupted straight S1 furrows; very short straight intercalating ring with small inflated lateral lobes; short occipital ring slightly projecting backwards; pygidium sub-hexagonal with truncated posterior and posterolateral outline, almost as long as half width, with short anterolateral edge, long axis; sculpture of spaced granules.

Remarks. – The new species shares with *Ch. clapassousensis* the very short and wide intercalating ring. It is distinct in having a straight configuration, similar to the type species, with a rectangular median lobe that remains below base of anterior glabellar lobe. In contrast, the S1 furrows are straight and thin abaxially, interrupted and almost effaced medially. The median lobe is uninflated and poorly separated from low lateral lobes, the occipital furrow transverse and only slightly set back behind lateral lobes, the occipital ring narrow, moderately vaulted and backwards projected, the posterior border furrow deeper than lateral border furrow.

The pygidium is distinct from all other species in its subhexagonal, posteriorly and posterolaterally slightly truncated outline, and the advanced position of maximum width. The axis is long and high, defined by axial furrows that converge moderately backwards adjacent to anterior three axial rings, less so thereafter and shallowing around obtusely rounded posterior tip. There are six straight, low, axial rings besides long end piece. Anterior inter-ring furrows are straight, others slightly sigmoidal, shallow medially, the first three reaching axial furrows. Hints of pseudo-articulating half-rings appear on rings 2–4. Postaxial field is very short. Pleural region is moderately vaulted, with weakly vaulted pleural ribs, defined by deep, almost straight pleural furrows that die out beyond inner two-thirds of pleural region. Interpleural furrows are indistinguishable. Particular sculpture of cephalon: drop-like, spaced tubercles, fine granules on occipital ring, posterior border and in genal angle; very fine, dense granulation on pygidium.

***Chlupacops narbonnensis* sp. nov.**
Figure 8A–F

Holotype. – Cephalon UM-IP 940, Col du Puech de la Suque, Montagne Noire, Frasnian Zone 5 (Fig. 8B).

Type horizon and locality. – Pink-grey crinoidal biomicrosparite, Col du Puech de la Suque, section CPS-E, bed 60, Frasnian Zone 5.

Etymology. – Narbonnensis [Lat.] = from the region of Narbonne.

Other material. – Paratypes: cephala UM-IP 941–943, pygidia UM-IP 944–945; additional material: nine cephala UM-IP 946, two pygidia UM-IP 947; all from type locality and horizon.

Diagnosis. – Cephalon long with narrow parabolic outline; glabella obtusely pointed anteriorly, long in front of S1; intercalating ring narrow, with inflated lateral lobes; high visual surface with 14 vertical rows of up to five lenses in a row; eye lobe encroaching onto lateral border, pygidium subtrapezoidal, axis remaining markedly distant from posterior margin, axial furrows of low convergence posteriorly, posterolateral edge framed with rim.

Remarks. – In comparison with the other species of *Chlupacops*, *C. narbonnensis* has the highest length/width ratios of the cephalon, the anterior glabella lobe and the intercalating ring. As such the cephalon is narrow-parabolic in outline and has a relatively narrow (tr.) intercalating ring. Consequently, the axial furrows have a relatively low angle of divergence. The anterior contour of the glabella is obtusely pointed, a feature that is attenuated in larger holaspides but does not occur in the other species. Small holaspid specimens are characterised by a relatively narrow anteriorly pointed glabella and deep outwardly-curved palpebral furrows. These features weaken in larger morphs. In addition, *C. narbonnensis* has

the highest number of vertical lens rows and lenses and the shortest postocular field. The intercalating ring is slightly curved transversely, markedly tripartite with inflated, subquadrangular lateral lobes separated from low median lobe by continuous exsagittal furrows. S1 is transverse, deep and straight abaxially, forwardly curved and shallow medially. Occipital furrow is continuously deep, gently curved forwards medially. Occipital ring is long (twice length of intercalating ring [sag.]) with anterior edge notched distally to define weak lateral occipital lobes. Similar to the type species, the eye lobe encroaches on the lateral border. The new species has a rather long (sag.) postvincular doublure that is likewise developed in *Ch. laticeps*, but is much shorter in all other species. Sculpture: small, spaced tubercles on dorsal surface; postvincular doublure with wavy, discontinous terrace ridges. Pygidium shares with *migrans* the subtrapezoidal outline, but has a shorter anterolateral edge with a more advanced level of maximum width. It is particular in having a rather short axis remaining markedly distant from the posterior edge. Lateral and posterior margins are framed with thin rim. Axial furrows are deep, converging stronger backwards anteriorly than posterior to 4th axial ring, not united posteriorly. Axial rings very low, straight, provided with pseudo-articulating half-rings. Interring furrows are straight, the anterior four reaching axial furrows. Pleural region moderately vaulted, with 5 moderately vaulted pleural ribs, defined by deep, scarcely curved pleural furrows that die out beyond inner two-thirds of pleural region. Interpleural furrows are discernible in anterior three ribs. Sculpture: very fine, spaced granules on adaxial parts of exoskeleton, distal parts of pleural fields smooth.

Genus *Girardina* gen. nov

Type species. – *Girardina konradbartzschi* sp. nov.

Etymology. – Dedicated to Catherine Girard for her outstanding research on Late Devonian conodonts in the Montagne Noire.

Diagnosis. – Cephalon of widely parabolic outline, glabella anteriorly high without overhang, very small eye lobe situated far anteriorly, low, with three aligned lenses, faint vincular furrow, long pygidium with slender axis remaining far from posterior margin, straight axial rings, marked axial furrows with posterior closure, pleural field with faint ribs and pleural furrows reaching posterolateral margin. Sculpture granulose.

Remarks. – The new genus shares with the slightly younger *Trimerocephaloides* Feist *et al.* (2009), from the Canning Basin area of NW Australia, reduction of the eye lobe and vincular furrow, long pygidium with axis remaining distant from posterior margin, low relief of pleural ribs and weak furrows. The Australian taxon, however, has an anteriorly low preoccipital glabella with gently sloping profile, no functional visual organ and abaxially deep vincular furrows. In addition, unlike *Girardina*, the tip of the pygidial axis is connected to a long, prominent postaxial ridge. Similarities between the new genus and the early Famennian *Dienstina* Richter & Richter, 1931 from the Rhenish Massif concern the short glabella anteriorly to intercalating ring, the small triangular eye lobe, the reduction of the vincular furrow, the short pygidial axis and the low convexity of the pleural field. *Girardina* has a more differentiated intercalating ring, a much higher anterior glabella and only three ocular lenses versus 35–40 in *Dienstina.* In addition, the pygidium of *Girardina* is much longer and has a narrower axis.

Occurrence. – Late Frasnian Zone 12 (Thuringia: Kahlleite; Montagne Noire: Causses-et-Veyran).

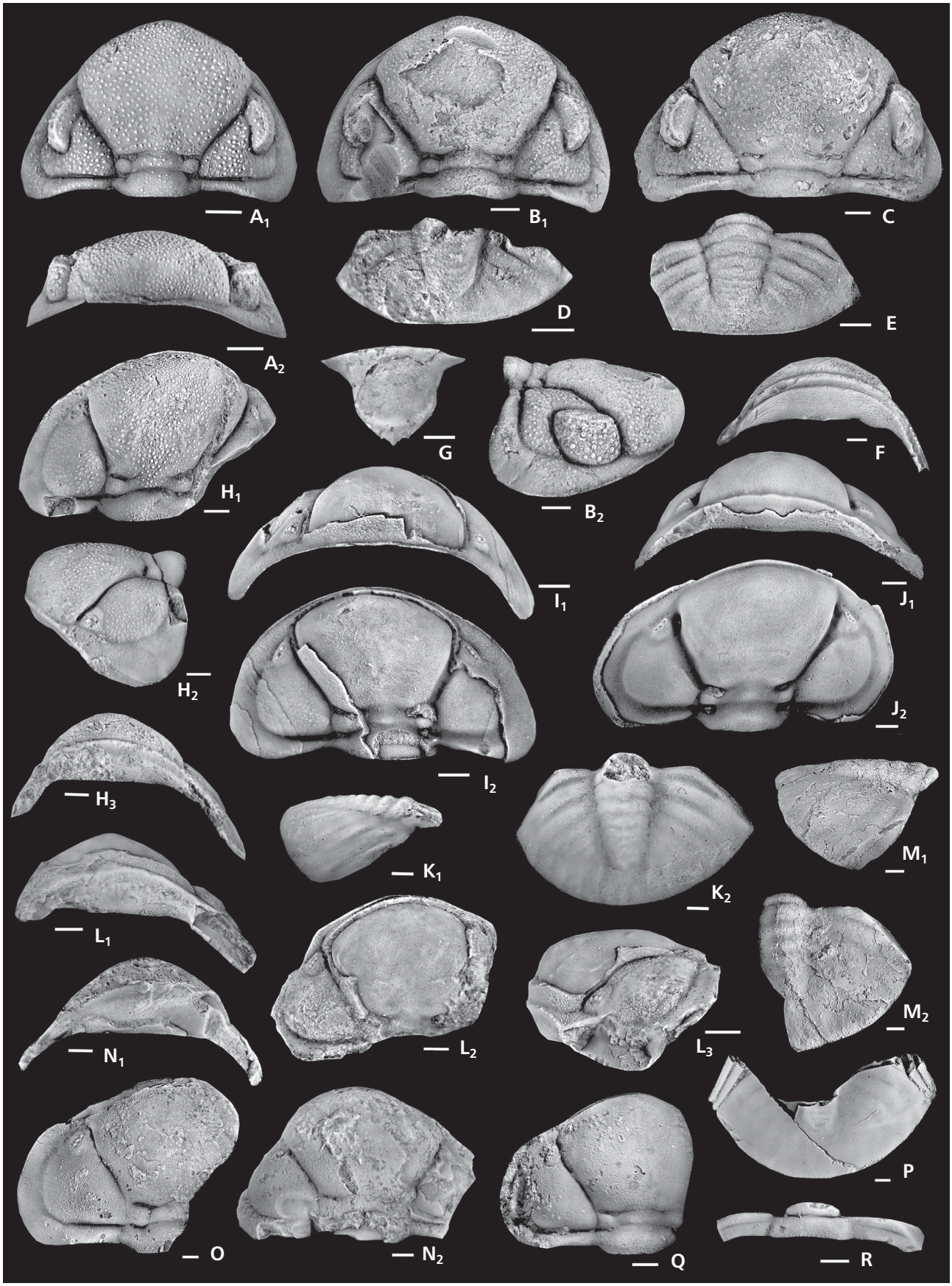
Species included. – *Girardina konradbartzschi* sp. nov., *G. consimilis* sp. nov.; included with question: *G.*? *liopyga* (Richter, 1863).

***Girardina konradbartzschi* sp. nov.**
Figure 8G–K

Holotype. – Cephalon UM-IP 948, Kahlleite (Thuringia), Frasnian Zone 12 (Fig. 8I).

Type horizon and locality. – Kahlleite quarry, light grey-

Figure 8. Specimens from Montagne Noire, France, except in G–K. • A–F – *Chlupacops narbonnensis* sp. nov., Col du Puech de la Suque; A – cephalon UM-IP 941, dorsal (A_1), anterior (A_2) views; B – holotype cephalon UM-IP 940, dorsal (B_1), lateral (B_2) views; C – cephalon UM-IP 942, dorsal view; D – pygidium UM-IP 944, dorsal view; E – pygidium UM-IP 945, dorsal view; F – cephalon UM-UP 943, ventral view. • G–K – *Girardina konradbartzschi* sp. nov., Kahlleite Quarry, Thuringia, Germany; G – hypostome UM-IP 951, internal mould, ventral view; H – fragmentary cephalon UM-IP 949, dorsal (H_1), lateral (H_2), ventral (H_3) views; I – holotype cephalon UM-IP 948, partially exfoliated, anterior (I_1), dorsal (I_2) views; J – exfoliated cephalon UM-IP 950, anteroventral (J_1), dorsal (J_2) views; K – pygidium UM-IP 952, exfoliated, lateral (K_1), dorsal (K_2) views. • L–R – *Girardina consimilis* sp. nov., Causses-et-Veyran; L – fragmentary cephalon UM-IP 956, ventral (L_1), dorsal (L_2), lateral (L_3) views; M – fragmentary pygidium UM-IP 960, cast of external mould, lateral (M_1), dorsal (M_2) views; N – fragmentary cephalon UM-IP 957, ventral (N_1), dorsal (N_2) views; O – holotype fragmentary cephalon UM-IP 955, dorsal view; P – fragmentary pygidium with relicts of two thoracic segments UM-IP 961, dorsal view; Q – incomplete cephalon UM-IP 858, cast of external mould, dorsal view; R – thoracic segment UM-IP 959, dorsal view. Scale = 1mm.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beige ostracod-rich, pyritic biodetrital calcilutite, "Ostracod-limestone" (Bartzsch *et al.* 1993), "Usseln Kalk" (Gereke 2007, pp. 72, 73).

Etymology. – After Konrad Bartzsch, Saalfeld, for his expert guidance in the field.

Other material. – Paratypes: cephala UM-IP 949–950, hypostome UM-IP 951, pygidium UM-IP 952; additional material: nine cephala (UM-IP 953), seven pygidia (UM-IP 954); all from type locality and horizon.

Diagnosis. – Cephalon with narrow genae, glabella with evenly curved anterior outline and obtusely rounded anterolateral angles, posterior borders adaxially shortening, pleural field of pygidium with distinct ribs and pleural furrows, medium-sized granular sculpture on adaxial parts of cephalon, pygidium smooth.

Description. – Cephalon of widely parabolic outline has a length/width ratio of 0.57, and an evenly arched transverse profile in anterior view. Its maximum width lies at level of intercalating ring. Glabella not protruding anteriorly; its anterior lobe in front of the intercalating ring has a length/width ratio of 0.72 and its length is 70% of cephalic length. It is of high transverse vault, with gently curved profile in lateral view except for strongly downcurved frontal face which is almost vertical, without overhang. Axial furrows are deep, straight between S1 and palpebral furrow subtending an angle of 64°, gently curved inwards anteriorly, and forming obtuse glabellar angles. Short, convex-forward S2 and S3 are discernible on internal mould. Narrow rim-like anterior border protrudes slightly. S1 is sigmoidal, continuous on internal mould, interrupted medially on external mould, with deep, slightly oblique apodemal pits that meet axial furrows. Intercalating ring long (sag.), equal to 35% of cephalic width and 61% of glabellar width. It is tripartite, with large, trapezoidal, moderately inflated lateral lobes and medially slightly swollen median lobe that merges anteriorly with base of anterior glabella on external mould, being separated from it by shallow, forwardly-curved S1 on internal mould. Occipital furrow evenly curved forwards medially. Occipital ring inflated, higher than base of anterior glabella, twice as long and of same transverse width as intercalating ring, markedly narrowing distally, without lateral lobes. Genal field is inflated, semielliptical, widest opposite S1, transverse width = 68% of intercalating ring, surrounded by gently curved lateral and posterior border furrows of even depth. Eye lobe is situated at anterior extremity of genal field, very small, subtriangular, low, and delimited by anterolateral border furrow. Palpebral furrow is very weakly impressed, continuously surrounding eye lobe between axial and border furrows. Visual surface is ill-defined carrying three prominent lenses aligned in an oblique row. Facial suture curves across anterolateral border to embrace ocular lenses before joining lateral border furrow; point ω is situated far forwards opposite posterior end of eye-lobe, thus defining a very short librigena. Posterior border, narrow at junction with occipital ring, considerably widens abaxially to merge without angle with lateral border. Borders inflated. Vincular furrow is barely discernible on external mould (*i.e.* Fig. 8H$_3$), narrow and weak on internal mould (*i.e.* Fig. 8J$_1$). Doublure is long (sag.), moderately vaulted, slightly sigmoidal in sagittal profile with gently curved hypostomal suture. Dorsal surface of cephalon with sculpture of medium-sized tubercles on adaxial parts, diminishing in size abaxially, lateral borders smooth; doublure with short, irregular wrinkles. Hypostome is as long as wide (without wings), with wide, evenly curved hypostomal suture; middle body uniformly vaulted, undifferentiated, rather wide (tr.) posteriorly; narrow lateral border and posteriorly extended triangular posterior border with three spines. Pygidium is long (length to width ratio = 0.6), of evenly rounded posterior outline, widest at level of fifth axial ring, with width of anterior articulating edge equal to 37% that of anterolateral edge, moderately and evenly vaulted in lateral and posterior views. Axis is slender with seven low axial rings besides end piece, obtusely pointed behind, not reaching posterior margin, and slightly curved in lateral view, merging with postaxial area. Axial furrows straight with closure around tip of axis. Inter-ring furrows straight and continuous, almost effaced on exterior of exoskeleton. Pleural field moderately vaulted with 5–6 flat ribs of which anterior two are more strongly vaulted, scarcely narrowing abaxially, backwardly curved distally to reach edge of posterolateral border. First pleural furrows are deep, remainder diminishing progressively rearwards but remain discernible until edges on internal mould, fading away on exterior of exoskeleton. No sculpture discernible on external mould.

Remarks. – Most individual sclerites are tectonically slightly distorted. Depending on preservation, features are different in their relief and outline on internal moulds and on the external surface, especially in the pygidium.

***Girardina consimilis* sp. nov.**
Figure 8L–R

Holotype. – Cephalon UM-IP 955, Causses-et-Veyran, Montagne Noire, Frasnian Zone 12 (Fig. 8O).

Type horizon and locality. – Brick-red biomicritic cephalopod limestone below Lower Kellwasser horizon, near section CV-S at 1 km NW of Causses-et-Veyran village (43° 28′ 46.26″ N, 5° 94′ 44.32″ E).

Etymology. – *Consimilis* [Lat.], very similar (to type species).

Other material. – Paratypes: cephala UM-IP 956–958, thoracic segment UM-IP 959, pygidia UM-IP 960–961, all from type locality and horizon.

Diagnosis. – Cephalon with broad genal fields, glabella with slightly pointed anterior contour and anterolateral angles, occipital ring long (exsag.) distally, adaxial parts of posterior border not narrowing, pleural field of pygidium with posteriorly effaced ribs and pleural furrows; dense, uniformly fine-grained granules on entire exoskeleton.

Remarks. – The new taxon from the Montagne Noire is identical with the type species in many aspects. Though the material is fragmentary a few particularly diagnostic features allow comparison with the type species. The preoccipital glabellar lobe of *consimilis* is anteriorly obtusely rounded and has more pointed and distally slightly extended anterior angles, the anterior course of the axial furrows remaining straight. The occipital ring is only slightly narrowing abaxially. The straight adaxial part of the posterior border does not become narrower proximally. The genal field though similar in vault and outline is much wider (tr.) reaching 78% of width of intercalating ring. Vincular furrow is perceptible as a long (sag.) rather shallow depression on external mould merging behind with strongly vaulted postvincular doublure. Pleural field of pygidium carries rather faint ribs and inter-rib furrows of which only the four anterior ones are barely perceptible on external surface. Sculpture consists of dense very small granules covering uniformly the entire exoskeleton, besides postvincular doublure with wrinkles. Features of thoracic segments are available for *consimilis*: the axial ring, devoid of lateral lobes, is wider (tr.) than pleura (1:0.86).

***Girardina*? *liopyga* (Richter, 1863)**

1863 *Phacops liopyga*; Richter, p. 669, pl. 19, figs 4, 5.
1926 *Phacopidella*? *liopyga*. – Richter & Richter, p. 204.
1954 *Phacopidella* cf. *liopyga*. – Pfeiffer, p. 48, pl. 3, figs 10, 11, pl. 6, fig. 1.
1959 *Phacopidella* (*Dienstina*) *liopyga*. – Pfeiffer, p. 271, pl. 4, fig. 6.

Remarks. – The originals of Richter (1863) being lost (*fide* Pfeiffer 1959), a neotype of the species was erected by Pfeiffer (1959), collected by him near to the type locality of Laasen. This specimen, a thoraco-pygidium and an inverted cephalon in Salter's position, bears features of *Dienstina* such as the forward-positioned small and low eye and the short pygidial axis. However, the eye has fewer (5–6, *fide* Pfeiffer 1959, p. 271) lenses which are not included in an elliptic visual surface, the intercalating ring is much shorter and tripartite, and the pygidium has a longer axis with more rings. In these features the species ressembles *Girardina*. However the higher number of eye lenses does not correspond to the diagnostic number of lenses that characterises the genus. Awaiting more and better preserved material of *liopyga*, we assign this species to *Girardina* with question.

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